

The Munich Specimen of *Triceratops* with a Revision of the Genus

By

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With 15 figures in the text, 12 plates
and 4 tables

ABSTRACT

The remarkable skull of *Triceratops*, the type specimen of *T. brevicornus*, was transferred from Yale Peabody Museum to the Bayerische Staatssammlung für Paläontologie und historische Geologie in 1964. That transfer is officially recorded here, together with detailed description and illustration. Re-examination of the history of *Triceratops* and the designation of the many species by Marsh, raises doubts about

their validity. Knowledge of the zoogeography of living large terrestrial animals, compared with the very localized occurrence of most of the type specimens of *Triceratops* argues further that in all probability only one species, *Triceratops horridus*, is present in current collections. The holotype is Y.P.M. 1820.

KURZFASSUNG

Der bemerkenswerte Schädel von *Triceratops*, dem Typus-exemplar von *T. brevicornus* Hatcher, wurde im Jahre 1964 vom Peabody Museum der Yale University in New Haven, U.S.A., an die Bayerische Staatssammlung für Paläontologie und historische Geologie in München abgegeben. In Verbindung mit einer detaillierten Beschreibung und Illustration des Schädels und des zu ihm gehörenden postcranialen Materials wird dieser Transfer hier offiziell bekanntgemacht.

Eine Überprüfung der Entdeckungsgeschichte von *Triceratops* und die Errichtung der vielen Arten durch Marsh läßt Zweifel an deren Gültigkeit aufkommen. Die Kenntnis der zoogeographischen Verbreitung heutiger, großer terrestrischer Tiere, verglichen mit dem sehr lokalen Vorkommen der meisten Typusexemplare von *Triceratops*, sprechen des weiteren dafür, daß aller Wahrscheinlichkeit nach in den heutigen Museumsbeständen nur eine Art, *Triceratops horridus* Marsh, vorhanden ist. Der Holotyp befindet sich im Yale Peabody Museum (Y.P.M. 1820).

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PART I. TRICERATOPS

INTRODUCTION

During the years from 1889 to 1892, a series of remarkable ceratopsian dinosaur specimens was collected by John Bell Hatcher for Yale College from the late Cretaceous rocks of east central Wyoming in strata then termed the Laramie beds, or later the "Ceratops beds". These strata are now formally referred to as the Lance formation and are of Maestrichtian age. Hatcher had heard of the discovery of a pair of very large fossil horns near Lusk, Wyoming. In the spring of 1889, he met a Mr. C.A. Guernsey of Douglas, Wyoming who had one of these horns in his possession. Hatcher was taken to the site where much of a skull was still imbedded in the rock. This specimen led Hatcher to explore the region around the site, with extraordinary results. The area was within what was then called Converse County — a region of vast badland exposures of the Lance formation. The area turned out to be unbelievably rich in ceratopsian remains — a group of horned dinosaurs unknown at the time. In the years that followed, Hatcher collected 32 partial to complete ceratopsian skulls, most of which were assigned to the genus *Triceratops*, just from this

restricted area of Converse County. The Munich specimen was one of those.

The Munich specimen was discovered by Mr. W.H. Utterback in the spring of 1891 at a site approximately 4.5 km upstream from the mouth of Lightning Creek and 2+ km south of that stream in Converse County. It was collected that summer by Hatcher, assisted by Utterback, A.L. Sullins and T.A. Bostwick, and shipped to Yale College Museum (now Yale's Peabody Museum of Natural History) in New Haven, Connecticut, where it was prepared for study. Hatcher's employer at Yale, Professor O.C. Marsh, had studied all previous ceratopsian finds and had concluded that Hatcher's previous specimens from Converse County were the first discovered remains of no less than nine different species, all of which were ultimately assigned to *Triceratops*. Preparation of this specimen was not completed until shortly before Marsh's death in 1899. Consequently, it was never studied by Marsh. Appropriately, as Marsh's protégé and premier collector, Hatcher himself studied this newly prepared and nearly per-

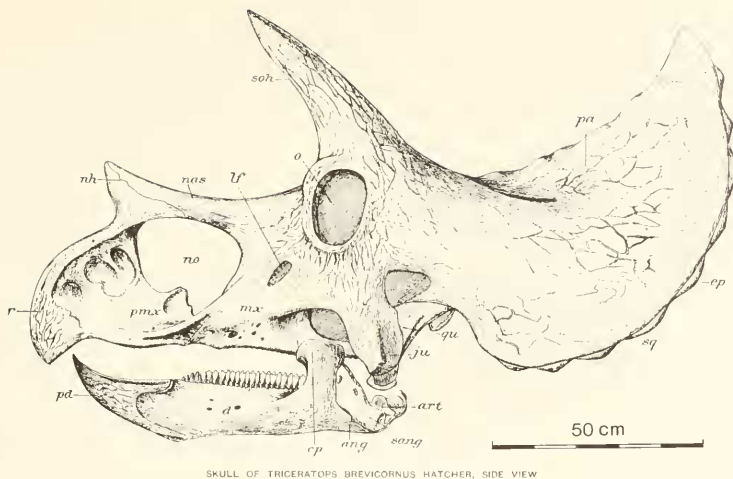


Fig. 1: *Triceratops "brevicornus"*, skull of type specimen (YPM 1834, now BSP 1964 I 458), as figured by Hatcher, Marsh & Lull 1907, plate 41.

fect skull and jaws (which occurred with part of the vertebral column), and in 1905, Hatcher defined this specimen as representing a new species of *Triceratops*, which he named *brevicornus* in reference to the shortness of the skull horns (see Figs. 1 and 2).

With the completion in 1926 of the present Peabody Museum at Yale, the skull of *T. brevicornus* was placed on public display together with many of the other type skulls of other *Triceratops* species from Converse County (now Niobrara County), Wyoming. Subsequent changes in the Peabody Museum exhibits required the removal of several of Yale's ceratopsian menagerie including *T. brevicornus*.

In 1963, Professor Dr. Richard Dehm, Director of the Bayerische Staatssammlung für Paläontologie und historische Geologie visited Yale's Peabody Museum and learned of Yale's "surplus" of ceratopsian skulls — nearly all of them from Hatcher's endeavors in Converse County. In search of exhibitable specimens for his own institute in Munich, Professor Dehm negotiated with Peabody Museum Director, Professor S. Dillon Ripley about such an acquisition. The result was the transfer of the Yale specimen of *Triceratops brevicornus* to the

State Collections of Bavaria in Munich, where it is on public display once again.

One purpose (of several) of this paper is to publicize this transfer; *Triceratops brevicornus*, formerly Y.P.M. 1834, is now officially B.S.P. 1964 I 458 in the Bavarian State Collections in Munich (Bayerische Staatssammlung für Paläontologie und historische Geologie).

In addition, we submit an up-dated description and illustrations of B.S.P. 1964 I 458 together with our assessment of the systematics of the genus *Triceratops*.

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Fig. 2: *Triceratops "brevicornus"*, presacral vertebral column of type specimen (YPM 1834, now BSP 1964 I 458), as figured by Hatcher, Marsh & Lull 1907, plate 40, fig. 1.

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Abbreviations

For the sake of brevity, institutional names are abbreviated as follows:

- A.M.N.H. — American Museum of Natural History, New York.
- B.S.P. — Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich.
- C.M.N.H. — Carnegie Museum of Natural History, Pittsburgh.
- F.M.N.H. — Field Museum of Natural History, Chicago.
- G.S.C. — Geological Survey of Canada, Ottawa.
- M.C.Z. — Museum of Comparative Zoology, Harvard, Cambridge.
- S.M. — Senckenberg Museum, Frankfurt.
- U.S.N.M. — United States National Museum, Smithsonian, Washington, D.C.
- Y.P.M. — Peabody Museum of Natural History, Yale, New Haven.

THE GENUS *TRICERATOPS*

For a name so well known, and a genus believed so well founded on incontestable specimens and published documentation, it may come as a surprise to learn that there is no adequate definition or diagnosis of the genus *Triceratops* in the published literature. Yet sixteen species and numerous specimens have been assigned to *Triceratops*, including the Munich specimen that is the primary subject of this study. This deficiency is in part a consequence of the historical sequence of events that led up to — and followed after — the first use of the name *Triceratops* and the subsequent application and systematic placement of that term. It would appear that workers after Marsh intuitively “knew” what *Triceratops* was, for no one really defined it or seemed to appreciate that no useful diagnosis had ever been formulated. We will present, in passing, the historical facts that contributed to this state of affairs.

The name *Triceratops* was originated by O.C. Marsh in August of 1889 (b) when he briefly described a ceratopsian skull, which he had defined (inadequately) four months earlier (Marsh, 1889a) as a new species (*horridus*) of the genus *Ceratops*. In proposing the name *Triceratops*, Marsh gave the following description:

“In addition to the pair of massive horn cores on the top of the skull, there is a third horn core on the nose. This is median, as in the Rhinoceros, and is placed on the end of the nasals, which are firmly coossified to support it. The edentulous premaxillaries are compressed anteriorly, and are strongly coossified with each other and with a third bone in front, which corresponds to the pre-dentary bone below, the whole forming a projecting beak, like that of a tortoise. Over all, there was, evidently, a huge horny covering, like the beak of a bird. The bone in front of the premaxillaries has apparently not before been observed in any vertebrate and may be called the rostral bone (os rostrale). — — — There is a huge occipital crest extending backward and outward. In the present specimen, this is bent downward at the sides, like the back part of a helmet, thus affording, in life, strong protection to the neck. The lower jaws are massive, and were united in front by a strong pre-dentary bone. This pointed anteriorly, and its surface

marked by vascular impressions, showing that it was covered with horn, and fitted to meet the beak above. The skull appears to have been at least two meters in length, aside from the horny beak. It represents a genus distinct from the type of the family, which may be called *Triceratops*.” (Marsh, 1889b, pp. 173–174.)

This “diagnosis” was sufficient in 1889 to distinguish *Triceratops* from all other then-known ceratopsians, but it is not definitive now. It applies equally well to at least five of the ten currently “accepted” genera of the Ceratopsidae! While subsequent refinements by Hatcher (1907), Lull (1907, 1933) and Steel (1969) have improved matters, these are still inadequate. Before we submit our revised diagnoses for the genus, it is informative to review the taxonomic history that led up to Marsh’s creation of *Triceratops*.

Excluding the first three-named ceratopsian genera (*Agathaumas*, *Polyonax* and *Monoclonius* (Cope 1872, 1874, 1876), all based on inadequate and now indeterminate fragments, the first event in the taxonomic evolution of *Triceratops* was the creation by Marsh (1887) of *Bison alticornus* named for a pair of large frontal horn cores (U.S.N.M. 1871E) from the Denver formation (Cretaceous, but mistakenly believed then to be Tertiary) of Colorado. The next year, Marsh (1888) established the binomial *Ceratops montanus* for another pair of frontal horn cores and an occipital condyle (U.S.N.M. 2411) from near the top of the Judith River beds (Cretaceous) of east-central Montana. In 1889(a), Marsh, now aware of the Cretaceous age of the Denver formation, implied that his *Bison alticornus* had been incorrectly identified. That implication concluded a brief paper in which he established a second species of *Ceratops*, *C. horridus*, based on the major part of a skull and partial lower jaw (Y.P.M. 1820) from low in the “Laramie” (= Lance) formation in Niobrara County, Wyoming. Later that same year (1889b) Marsh formally transferred *Bison alticornus* to *Ceratops* — in the same paper in which he proposed the genus *Triceratops*

with *horridus* the type species. During the next several months, Marsh named six more species of *Triceratops* and at the end of 1891 the ceratopsian roster consisted of:

Agathaumas sylvestris Cope, 1872
Polygonax mortuarius Cope, 1874
Monoclonius crassus Cope, 1876
Ceratops montanus Marsh, 1888
Ceratops alticornus Marsh, 1887
Triceratops horridus Marsh, 1889
Triceratops flabellatus Marsh, 1889
Triceratops galeus Marsh, 1889
Triceratops serratus Marsh, 1890
Triceratops prorsus Marsh, 1890
Triceratops sulcatus Marsh, 1890
Triceratops elatus Marsh, 1891
 plus the new genus
Torosaurus latus Marsh, 1891.

Thus, in the space of less than 30 months, Marsh established his *Triceratops* dynasty, of which most species are still recognized, even if not tested. It is our intention to test the registered species of *Triceratops* and report our conclusions.

In order to meet the above objective, it is essential that we know what *Triceratops* is. Despite the announcements of many new species of *Triceratops* in the years after 1889, Hatcher (1907) was the first to provide further definition of the genus listing the following distinctive conditions:

- 1) Supraorbital horns directed forward and upward at an angle of 45 degrees.
- 2) Nasal horn of moderate length and directed nearly straight forward.
- 3) No parietal fontanelles.
- 4) Squamosal short and broad.

In the same monograph, Lull (1907) added the following:

- 1) Supraorbital horn cores slender to robust, ovate in section.
- 2) Orbit elliptical with long axis inclined down and forward.
- 3) Parietals convex laterally, somewhat concave upward along long axis, much expanded posteriorly and narrowing anteriorly. Very thin in the center and thickened along the borders and the mid-line.
- 4) Squamosals stout and broad, constituting half of crest area.
- 5) Vascular markings on upper crest surface of some and along the lateral regions of the crest undersurface.

Lull (1933) did not give a concise definition of the genus, but instead listed "The common factors which may be used are": citing size (always considering the indicated individual age), skull proportions (long or short muzzle, broad or narrow crest), the condition of particular bones and other features (rostrum, jugal, jugal notch, orbit, infratemporal fenestra, nasal and brow horns and vascular impressions on the crest). In fact, none of these characters are definitive of the genus. Rather they have been cited in defining or distinguishing the several species of *Triceratops*. Steel (1969) also simply repeated specific characters (which he identified as such), adding only a single new generic character — epoccipitals. But epoccipital bones are known in other ceratopsians (*Chasmosaurus*, *Monoclonius*).

A revised diagnosis of the genus *Triceratops* is presented here and in the section on systematics in this study.

Diagnosis: Large ceratopsian of more than 6 m length up to 8 or more meters. Skull distinctive bearing elongate supraorbital horn cores plus a single variable nasal horn core. Brow horns vary in taper, stoutness, curvature and length, but generally project up and moderately forward as well as laterally. Nasal horn varies from a modestly tapered blunt boss to a prominent upward and forwardly directed projection. Nasal horn always much shorter than brow horns. Brow horns never longer than pre-orbital skull length and usually distinctly shorter. Skull elongate with post-orbital length always greater than pre-orbital length, often close to 150% of pre-orbital length. Parietal-squamosal frill relatively short (compared to some other genera) and generally curves back and upward. The frill is never fenestrated (except by the small and highly variable supra- and lateral temporal fenestrae of all archosaurs). Frill margin may be ornamented by blunt, scallop-like epoccipital bones. Horns or spikes are never present on frill margins or jugal flanges. Where known, post-cranial features and counts are comparable to those of other large Late Cretaceous ceratopsian genera.

A BRIEF HISTORY OF CERATOPSIAN SYSTEMATICS

The family Ceratopsidae was established by Marsh (1888, p. 478) after studying the remains of his latest new genus and species *Ceratops montanus*. That specimen (U.S.N.M. 2411) consisted of two large brow horn cores and an associated occipital condyle that had been collected by J. B. Hatcher from the Judith River beds of Montana. In reporting on that specimen, Marsh noted that teeth, vertebrae and limb bones "which probably belong to the present genus" were all secured in the same horizon. He remarked "They indicate a close affinity with *Stegosaurus*, which was probably the Jurassic ancestor of *Ceratops*." These additional remains led Marsh to conclude:

"The remains at present referred to this genus, while resembling *Stegosaurus* in various important characters, appear to represent a distinct and highly specialized family that may be called the Ceratopsidae." (Marsh, 1888, p. 478.)

Notice that at this time, Marsh had not yet publically recognized the ceratopsian affinity of "*Bison*" *alticornus*. Therefore, he established this new family solely on the basis of the fragments of *Ceratops montanus* and those "other remains" (resembling *Stegosaurus*) that he believed to belong to *Ceratops*.

The following year, Marsh provided a detailed account of the ceratopsian skull, describing the (until then, incompletely published) anatomy of the skull and jaws of *Triceratops*. This was possible because new specimens had arrived from Hatcher in Wyoming, and on these Marsh had erected the genus *Triceratops*, transferring an earlier species (*horridus*) as the type species, and named two new species (*flabellatus* and *galeus*). On the basis of this new material he listed the unique characters of the Ceratopsidae:

- "(1) The presence of a rostral bone, and the modification of the pre-dentary to form a sharp, cutting beak.
- (2) The frontal horn cores, which form the central feature of the armature.
- (3) The huge, expanded parietal crest.
- (4) The epoccipital bones.
- (5) The aborted transverse bone.

These are all features not before seen in the *Dmosauria*, and show that the family is a very distinct one." (Marsh, 1889c, p. 505.)

In 1890, Marsh finally realized how very different these horned dinosaurs were from all other dinosaurs (he had named two more species of *Triceratops* [*serratus* and *prorsus*] just four months earlier) and he proposed their recognition as a distinct sub-order of his order Predentata (= Ornithischia):

"the group is a very distinct one, worthy to be called a sub-order, which may be termed the Ceratopsia." (Marsh, 1890b, p. 418.)

He then listed the distinguishing features that separate the Ceratopsia from all other known major dinosaur kinds:

- "(1) The skull surmounted by massive horn-cores.
- (2) A rostral bone forming a sharp, cutting beak.
- (3) The teeth with two distinct roots.
- (4) The anterior cervical vertebrae coössified with each other.
- (5) The pubis projecting in front, and no post-pubis." (Marsh, 1890b, p. 421.)

In that same paper, Marsh named his sixth species of *Triceratops* – *sulcatus*.

Earlier that year, Marsh gave an expanded summary of the skeletal features that distinguished the family, in which he included details of the post-cranial anatomy for the first time. Those characters were:

- "(1) The atlas and axis, and one or more adjoining cervical vertebrae are coössified with each other.
- (2) Their cervical ribs are likewise firmly united with the same vertebrae.
- (3) The remaining cervical vertebrae are short, and have the articular faces of the centra nearly flat.
- (4) The trunk vertebrae have very short centra, with flat articular ends. Above the centra, they resemble the vertebrae of *Stegosaurus*.
- (5) The sacrum was strengthened by union with several adjacent vertebrae.
- (6) The caudal vertebrae are short and rugose, and the tail was of moderate length.
- (7) The ilium is elongated, especially in front; the ischium slender, and directed backward.
- (8) The pubis extended forward, and its posterior branch was wanting.
- (9) The limbs were short and massive, and all four were used in locomotion.
- (10) The feet were all provided with broad hoofs, as in *Stegosaurus*.
- (11) The bones of the skeleton all appear to have been solid.
- (12) Dermal ossifications were present, and some species were protected by heavy armor." (Marsh, 1890a, p. 83.)

In September of 1890, Marsh presented a detailed account of the osteology of his Ceratopsidae to the British Association for the Advancement of Science. This was subsequently published in the United States in the American Journal of Science (Marsh, 1891a). Later that year, the same journal contained a condensed summary of:

"The main characters which separate the group from all other known families of the *Dmosauria* are as follows:

- (1) A rostral bone, forming a sharp cutting beak.
- (2) The skull surmounted by massive horn cores.
- (3) The expanded parietal crest, with its marginal armature.

- (4) A pineal foramen.
- (5) The teeth with two distinct roots.
- (6) The anterior cervical vertebrae coössified with each other.
- (7) The dorsal vertebrae supporting, on the diapophysis, both the head and the tubercle of the rib.
- (8) The lumbar vertebrae wanting." (Marsh, 1891b, p. 341.)

Marsh's early alliance of the first ceratopsian remains with *Stegosaurus* appears to have been heavily influenced by his belief that the "other remains" found in the same horizon with *Ceratops montanus* included "some peculiar large dermal plates, in pairs, that indicate a well-ossified armor." His belief was further supported by the similarities Marsh saw in the vertebral neural arches and the hoof-like form of the unguals. Most likely, associated dermal plates were isolated scutes of the several Cretaceous ankylosaurs known now. But at that early date, and with such limited evidence, Marsh could not have known that some of the "other remains" actually belonged to other dinosaurian kinds not yet known well enough to separate from the ceratopsian remains. For example, see Pl. X of his 1891 address to the British Association, in which scutes and spines, clearly of ankylosaurian and pachycephalosaurian origins, are attributed to *Triceratops*. That same plate with the same taxonomic assignments is repeated in Marsh's 1896 "Dinosaurs of North America". Not until after the turn of the century were sufficient remains available to demonstrate that a distinct group of armored ornithischian dinosaurs co-existed with the ceratopsians, and the Suborder Ankylosauria was finally designated by v. Huene in 1914 (there spelled Ancylosauria).

Marsh (1896) included the following genera in his family Ceratopsidae: *Triceratops*, *Torosaurus*, *Sternholophus*, *Agathaurus*, *Monoclonius*, *Ceratops*, *Polyonax* and (the European) *Struthiosaurus*. Since that work, numerous additional specimens, some representing new taxa, have been recovered. These have been treated in the monographic studies by Hatcher, Marsh and Lull (1907) and Lull (1933), and in numerous later references. Currently, the Suborder Ceratopsia is recognized, represented by two families constituted as follows:

Class Reptilia
Subclass Archosauria
Order Ornithischia Seeley 1888
Suborder Ceratopsia Marsh 1890

Family Protoceratopsidae Granger and Gregory 1923

Bagaceratops, *Leptoceratops*, *Microceratops*, *Montanoceratops*, *Protoceratops*.

Family Ceratopsidae Marsh 1888

Agathaurus, *Anchiceratops*, *Arrhinoceratops*, *Brachyceratops*, *Ceratops*, *Chasmosaurus*, *Eoceratops*, *Monoclonius*, *?Notoceratops*, *Pachyrhinosaurus*, *Pentaceratops*, *Styracosaurus*, *Torosaurus*, *Triceratops*.

Several authors (Romer, 1956; Steel, 1969) have noted the apparent affinities of the Psittacosauridae to ceratopsians, and Protoceratopsidae in particular. Maryánska and Osmólska (1975) considered the Psittacosauridae as an early and highly specialized family of the Ceratopsia. Coombs (1980) advocated the transfer of this group from the Subclass Ornithopoda

to the Ceratopsia. Sereno (1984, 1986) listed psittacosaur as primitive ceratopsians. Though not yet widely adopted, we

believe this transfer should be accepted and therefore list this as a third family.

Family Psittacosauridae Osborn 1923

Protiguanodon, *Psittacosaurus*.

Table 1:
HISTORICAL RECORD OF *TRICERATOPS* AND RELATED
CERATOPSIAN TAXA

(Parenthetic numbers at left = Hatcher's Lance Cr. specimens)

A tabular summary of the recorded historical discoveries of ceratopsian specimens that played an important role in the evolution of the systematics of *Triceratops*. Please note that there are many other specimens that are attributed to *Triceratops*, such as the *T. calicornis* skull at the Field Museum and the *T. brevicornis* skull at Carnegie Museum and many others. These have not been included here because none were ever established as name-bearers.

Date & Sequence	Name Here	Catalogue Nr.	Original Name	Initial Designation	Status here	Original Site	Formation
Nr. 1 1872	<i>Agathaumas sylvestris</i>	AMNH 4000	Same	Holotype	nomen dubium	Black Butte Wyoming	Lance
Nr. 2 1874	<i>Polyonax mortuarius</i>	AMNH 3950	Same	Holotype	nomen dubium	„Colorado“	Laramie?
Nr. 3 1876	<i>Monoclonius crassus</i>	AMNH 3998	Same	Holotype	Holotype	Missouri R. Montana	Judith R.
Nr. 4 1887	<i>Triceratops alticornus</i>	USNM 1871E	<i>Ceratops alticornus</i>	Holotype <i>Bison alticornus</i>	nomen dubium	Green Mtn Creek	Denver beds
Nr. 5 1888	<i>Triceratops montanus</i>	USNM 2411	<i>Ceratops montanus</i>	Holotype	nomen dubium	Cow Creek Montana	Judith R.
Nr. 6 (1) 1889	<i>Triceratops horridus</i>	YPM 1820	<i>Triceratops horridus</i>	Holotype	Holotype	Buck Creek Wyoming	Lance
Nr. 7 (2) 1889	<i>Triceratops horridus</i>	YPM 1821	<i>Triceratops flabellatus</i>	Holotype	Synonym	Lance Creek Wyoming	Lance
Nr. 8 1889	<i>Triceratops</i> sp.	USNM 2410	<i>Triceratops galeus</i>	Holotype	nomen dubium	Colorado	Denver beds
Nr. 9 (3) 1890	<i>Triceratops horridus</i>	YPM 1822	<i>Triceratops prorsus</i>	Holotype	Synonym	Lightning Creek, Wyo.	Lance
Nr. 10 (4) 1890	<i>Triceratops horridus</i>	YPM 1823	<i>Triceratops serratus</i>	Holotype	Synonym	Lightning Creek, Wyo.	Lance
Nr. 11 (5) 1890	<i>Triceratops horridus</i>	USNM 4276	<i>Triceratops sulcatus</i>	Holotype	nomen dubium	Lance Creek Wyoming	Lance
Nr. 12 (6) 1890	<i>Triceratops horridus</i>	USNM 2416	<i>Triceratops serratus</i>	—	Synonym	Buck Creek Wyoming	Lance
Nr. 13 (7) 1890	<i>Triceratops?</i> <i>horridus</i>	USNM ? (Lost)	?	—	—	Buck Creek Wyoming	Lance
Nr. 14 (8) 1890	<i>Triceratops horridus</i>	USNM 5738	<i>Triceratops</i> sp.	—	Synonym?	Lance Creek Wyoming	Lance
Nr. 15 (9) 1890	<i>Triceratops horridus</i>	USNM 4720	<i>Triceratops obtusus</i>	Holotype	Synonym	Buck Creek Wyoming	Lance
Nr. 16 (10) 1890	<i>Triceratops horridus</i>	USNM 5741	<i>Triceratops elatus</i>	—	Synonym	Buck Creek Wyoming	Lance
Nr. 17 (11) 1890	<i>Triceratops horridus</i>	USNM 4708	<i>Triceratops elatus</i>	—	Synonym	Buck Creek Wyoming	Lance
Nr. 18 (12) 1890	<i>Triceratops horridus</i>	USNM 4286	<i>Triceratops sulcatus</i>	—	Synonym	Buck Creek Wyoming	Lance
Nr. 19 (13) 1890	<i>Triceratops horridus</i>	USNM 2124	<i>Triceratops</i> sp.	—		Buck Creek Wyoming	Lance

Date & Sequence	Name Here	Catalogue Nr.	Original Name	Initial Designation	Status here	Original Site	Formation
Nr. 20 (14) 1891	<i>Triceratops horridus</i>	USNM 7239	<i>Triceratops</i> sp.	—		Lance Creek Wyoming	Lance
Nr. 21 (15) 1891	<i>Triceratops horridus</i>	USNM 1208	<i>Triceratops sulcatus</i>	—	Synonym	Lance Creek Wyoming	Lance
Nr. 22 (16) 1891	<i>Triceratops horridus</i>	USNM 1201	<i>Triceratops elatus</i>	Holotype	Synonym	Lance Creek Wyoming	Lance
Nr. 23 (17) 1891	<i>Triceratops horridus</i>	USNM 1205	<i>Triceratops prorsus</i>	—	Synonym	Buck Creek Wyoming	Lance
Nr. 24 (18) 1891	<i>Triceratops horridus</i>	YPM 1829	<i>Triceratops elatus?</i>	—	Synonym	Cow Creek Wyoming	Lance
Nr. 25 (19) 1891	<i>Torosaurus latus</i>	YPM 1830	<i>Torosaurus latus</i>	Holotype	Holotype	Cow Creek Wyoming	Lance
Nr. 26 (19a) 1891	<i>Torosaurus gladius</i>	YPM 1831	<i>Torosaurus gladius</i>	Holotype	Holotype	Cow Creek Wyoming	Lance
Nr. 27 (20) 1891	<i>Triceratops horridus</i>	YPM 1833	<i>Triceratops hatcheri</i>	—	Synonym	Lance Creek Wyoming	Lance
Nr. 28 (21) 1891	<i>Triceratops horridus</i>	YPM 1832	<i>Triceratops brevicornus</i>	—	Synonym	Lightning Creek, Wyo.	Lance
Nr. 29 (22) 1891	<i>Triceratops horridus</i>	YPM 1834	<i>Triceratops brevicornus</i>	Holotype	Synonym	Lightning Creek, Wyo.	Lance
Nr. 30 (23) 1891	<i>Triceratops horridus</i>	YPM 1836	<i>Triceratops</i> sp.	—	Synonym?	Lance Creek Wyoming	Lance
Nr. 31 (24) 1892	<i>Triceratops horridus</i>	YPM 1828	<i>Triceratops „ingens“</i>	Holotype	nomen nudum	Dogie Creek Wyoming	Lance
Nr. 32 (25) 1892	<i>Triceratops horridus</i>	USNM 2412	<i>Triceratops hatcheri</i>	Holotype	Synonym?	Lance Creek Wyoming	Lance
Nr. 33 (26) 1892	<i>Triceratops horridus</i>	USNM 2100	<i>Triceratops prorsus</i>	—	Synonym	Lance Creek Wyoming	Lance
Nr. 34 (27) 1892	<i>Triceratops horridus</i>	USNM 5740	<i>Triceratops</i> sp.	—	Synonym?	Dogie Creek Wyoming	Lance
Nr. 35 (28) 1892	<i>Triceratops horridus</i>	USNM 6679	<i>Triceratops</i> sp.	—	Synonym?	Buck Creek Wyoming	Lance
Nr. 36 (29) 1892	<i>Triceratops horridus</i>	USNM 4928	<i>Triceratops calicornis</i>	Holotype	Synonym	Lance Creek Wyoming	Lance
Nr. 37 (30) 1892	<i>Triceratops horridus</i>	YPM 1837	<i>Triceratops</i> sp.	—	Synonym?	Dogie Creek Wyoming	Lance
Nr. 38 (31) 1892	<i>Triceratops horridus</i>	YPM 1838	<i>Triceratops</i> sp.	—	Synonym?	Lance Creek Wyoming	Lance
Nr. 39 1909	<i>Triceratops</i> sp. ?	AMNH 5040	<i>Triceratops maximus</i>	Holotype	nomen dubium	Rock Creek Montana	Hell Creek
Nr. 40 1934	<i>Triceratops horridus</i>	MCZ 1102	<i>Triceratops eurycephalus</i>	Holotype	Synonym	Goshen City Wyoming	Lance
Nr. 41 1946	<i>Triceratops horridus</i>	GSC 8862	<i>Triceratops albertensis</i>	Holotype	Synonym	Red Deer R. Alberta	Edmonton

DISCOVERY AND NAMING OF *TRICERATOPS* “*BREVICORNUS*”

The holotype specimen of *Triceratops brevicornus*, B.S.P. 1964 I 458 (formerly Y.P.M. 1834) was discovered by W.H. Utterback in 1890 near Lusk, Wyoming. Utterback, A.L. Sullins and T.A. Bostwick assisted J.B. Hatcher in collecting this nearly complete skull and jaws and the incomplete post-cranial remains during the summer of 1891. Marsh did not live to

complete a study of the specimen, the task falling to Hatcher. Hatcher (1905) concluded that this specimen (his skull nr. 22) was distinct from all the earlier specimens he had recovered from Niobrara County and established the new species “*brevicornus*”. Another skull (nr. 21), Y.P.M. 1832 from nearby was judged to be of the same kind and was informally labeled as “plesiotype”. The criteria upon which Hatcher distinguished his new species are summarized in Part II of this study.

DESCRIPTION OF *TRICERATOPS* "BREVICORNUS"

B.S.P. 1964 I 458

LOCALITY AND STRATIGRAPHIC DATA

The type specimen of *Triceratops brevicornus* was collected during the summer of 1891 by J.B. Hatcher, its discoverer W.H. Utterback, and A.L. Sullins and T.A. Bostwick. Hatcher recorded the locality as "3 miles above the mouth of Lightning Creek and about 1 and 1/2 miles south of that stream in Converse County, Wyoming". That places it in the northeast quarter of Section 15, T. 37 N, R. 65 W, approximately 30 miles (44 km) NNW of Lusk, Niobrara County, Wyoming. A search of the field records in the Peabody Museum at Yale failed to turn up any description or sketch of the site, so it is not possible to pin point the location more precisely. It should be noted that according to Hatcher's map (1896), the site lies close to the center of the cluster of Hatcher sites that produced thirty skulls of *Triceratops* and two skulls of *Torosaurus* between 1889 and 1892. The most distant of these from the *T. brevicornus* site is approximately 15 miles (23 km) to the northeast — the site of the plesiotype of *T. prorsus* (U.S.N.M. 2100). The nearest other site is about 1 & 1/2 miles (2.3 km) to the west, which produced the plesiotype of *T. brevicornus* (Y.P.M. 1832) (see Fig. 15).

Hatcher reported that the producing "horizon was near the summit of the Laramie", but of course that is inadequate now. The precise stratigraphic level can no longer be established. Hatcher estimated the thickness of the Laramie *Ceratops* Beds in that region to be approximately 3000 feet (1000 m). But Knowlton (1909) concluded that it could not be more than 2000 feet (660 m). Knowlton also noted that the fossiliferous part of the *Ceratops* Beds is mainly the upper part some 100 to 150 feet below the overlying Fort Union formation. Malcolm McKenna (personal comm.) estimates a total thickness of about 3800 feet, of which approximately 1300 are exposed at the surface in the Niobrara County region. He further estimates that the Lance formation accumulated during an interval not in excess of 3 to 4 million years. Later reference to these data occur in Part III of this study.

DESCRIPTION OF SKULL AND MANDIBLES

(Plate 1)

The Munich skull is one of the more complete and better preserved specimens known of *Triceratops*, yet many of the desired details are unclear. In particular, virtually all of the sutures are indecipherable due to closure and fusion between cranial elements. That condition has been attributed (probably correctly) to extreme age by both Hatcher (1905) and Lull (1933). If that is correct, then the size of this specimen takes on special significance. Its maximum longitudinal (horizontal ?) dimension is 157 cm, which is significantly shorter than the 190+ cm average length of *Triceratops* skulls. In fact, there are larger specimens (*T. serratus*, Y.P.M. 1823; *T. elatus*, U.S.N.M. 1201) which display open cranial sutures and for that reason have been judged as not fully adult. This raises a

critical question: are size together with suture condition reliable indices of taxonomic difference? Are we secure in concluding that *T. brevicornus* is specifically distinct from *T. serratus* or *T. elatus* because of its distinctly smaller "adult" size? We think not.

The Munich skull features all the prescribed *Triceratops* characters: three forwardly-directed horns, one above each orbit and a much smaller medial horn on the nasals just behind the premaxillaries and directly above the anterior limit of the external nares; a moderately long posterior cranial crest constructed of the parietals¹⁾ and squamosals projecting back and upward over the anterior cervical region; the parietal-squamosal crest (frill) is not fenestrated; this frill lacks horns or spikes along the frill margin and on the frill surface. All other anatomical conditions displayed in this skull are normal ceratopsian features that are not limited to the genus *Triceratops*: laterally compressed median beak-like and unique rostral bone that is edentulous; a matching edentulous beak-like predentary on the mandible; edentulous premaxillaries; massive maxillaries and dentaries that carried large elongate dental batteries for shearing; a very large external narial opening; laterally directed orbit at the base of the brow horn that is circumscribed by robust and rugose margins; antorbital fenestra is small and slit-like, descending forward away from the orbit; both lateral and supratemporal fenestrae are small, the latter slit-like on the antero-dorsal surface of the frill; the jugal projects ventrally into a robust descending projection that overlaps the quadrate laterally.

Additional non-diagnostic features of this specimen are: the brow horns are relatively short and stout, but not nearly as robust as has been described and pictured (Pl. XLI, Hatcher, Marsh and Lull, 1907); the brow horns are more nearly circular than oval in section throughout their length and are directed up and forward with very little anterior or lateral curvature; the nasal horn is also short, laterally compressed, and directed up and forward (the transverse horn-splitting "suture" illustrated by Hatcher 1907 is a post-burial fracture); the narrowly elliptical antorbital fenestra (=lachrymal foramen of early authors) forms a deep channel that leads up and back toward the orbit; the lateral temporal fenestra is triangular in shape; the orbit is slightly oval to almost circular in outline; epoccipitals are present at a few places firmly co-ossified with the frill margins of the squamosals and parietals; a nearly circular opening described as the postfrontal fontanelle by Hatcher (1907) is situated in the mid-line just behind the brow horn bases, but as preserved it is not entirely certain that this is a natural opening; the base of the frill is supported by robust lateral expansions of the exoccipitals; this occipital region (quadrate, exoccipital and squamosal) is much compressed antero-posteriorly; preservation of the frill, which apparently was badly fractured into numerous small pieces, does not retain a clear-cut pattern of vascular channels as has been illustrated in past illustrations of this specimen; the occipital condyle is large and almost spherical and tilted slightly downward.

1) Discussion of this is deferred to the section on the parietal.

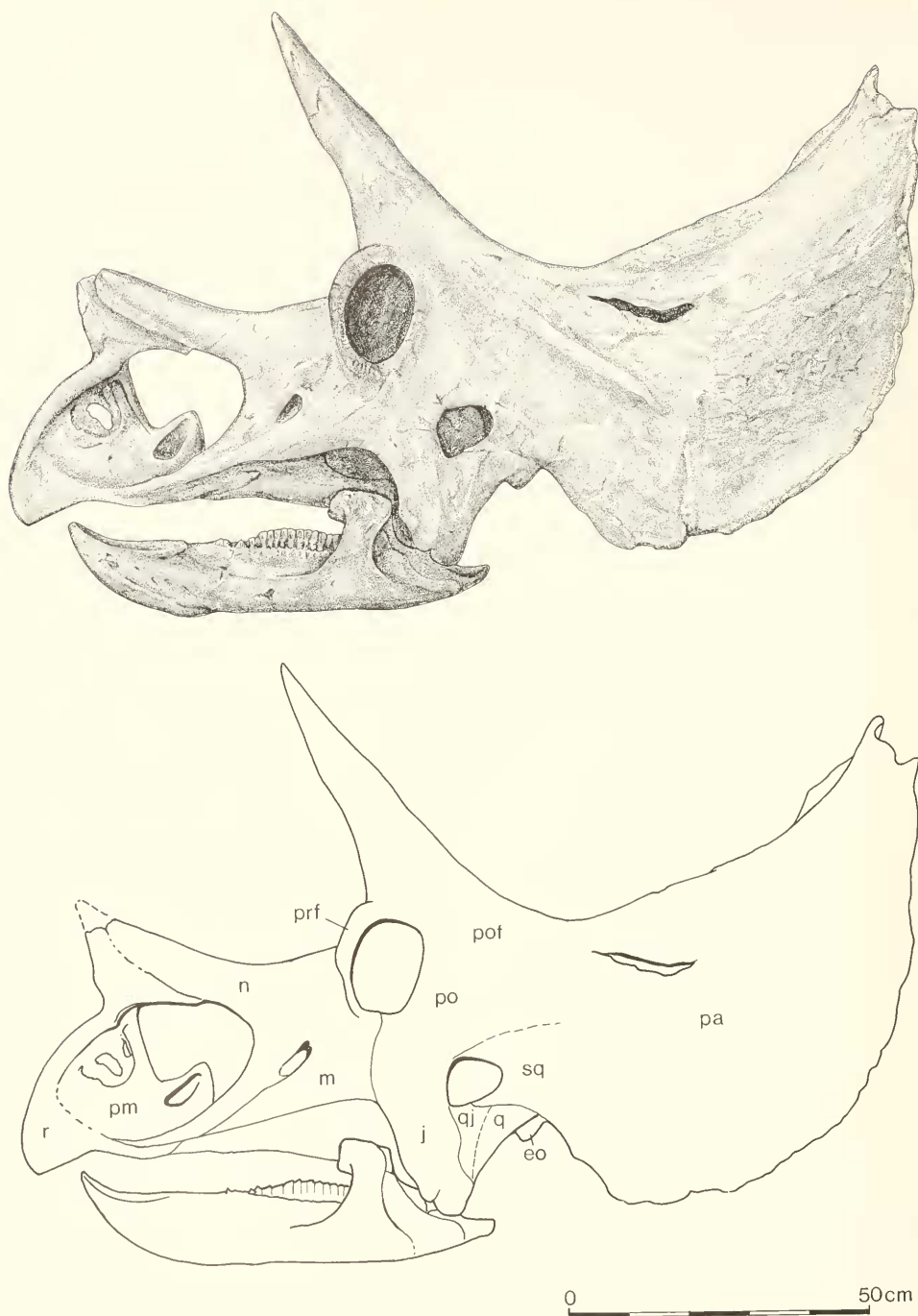


Fig. 3: *Triceratops* "brevicornus", skull of type specimen with skull elements indicated as follows: eo exoccipital, j jugal, m maxilla, n nasal, pa parietal, pm premaxillary, po postorbital, pof postfrontal, prf prefrontal, q quadrate, qj quadratojugal, r rostral, sq squamosal.

Skull

Rostral. In lateral view, this bone features a uniformly curved anterior profile descending from just in front of the nasal horn core to a moderately sharp, but not hooked, beak apex. This is one of the most distinctive features of *Triceratops*. The ventral margin is nearly straight, with only a slightly concave outline. As preserved, the inferior margins are not sharp-edged, but the rostral is deeply excavated ventrally. It is greatly compressed laterally, with a narrow wedge-shape when viewed from above. No sutures are detectable between it and the premaxillaries, nor is there any evidence whatsoever of a mid-line suture. In this specimen at least, it appears to be a true median element. Its surfaces are markedly rugose with vascular channels throughout, evidence of a covering horny beak.

Premaxillary. Firmly fused to the rostral are the paired premaxillaries which border the anterior and ventral margins of the large external nares. No sutures are recognizable between these elements or between them and either the rostral or the maxillaries. In contrast to the rostral, the surfaces are not textured, but rather are smooth with infrequent and minor vascular markings. In lateral view it is roughly L-shaped, but with a conspicuous parallelogram-shaped and well-defined fossa immediately in front of the large narial opening. The inferior margin is straight and robust.

Maxilla. This element is roughly triangular in lateral aspect, with the obtuse apex uppermost. Again, due to the advanced age of the individual, no certifiable sutures are discernible. The lower external surface slopes down and outward, descending from a prominent shelf or overhang that continues posteriorly to the jugal. This jugal-maxilla overhang is situated lateral to the coronoid process of the mandible and encloses that process when the jaws are closed. The lower external surface of the maxilla is smooth, but is penetrated by several prominent foramina. The upper external surface, that above the lateral overhang, is convex laterally and forms the lower margin of the antorbital fenestra. This surface is marked by faint but distinct vascular markings. No teeth are retained in either maxilla, but the alveolar channels are preserved, their lengths are approximately 36 to 38 cm and the number of tooth positions appears to be 30.

The antorbital fenestra is a conspicuous oval slit-like opening along, or close to, the upper margin of the maxilla. It measures approximately 7.0×3.5 cm in superficial dimensions and is oriented at approximately 45 degrees to the maxillary inferior margin. It leads to a narrowing canal that extends back and upward apparently into the orbital cavity. As noted elsewhere, earlier workers termed this the lachrymal foramen and its position and pathway suggest that it may be the same as that foramen in other archosaurs.

Nasal. Because of the obscured sutures, the limits of this bone cannot be defined. These elements are fused together and to the adjoining rostral, premaxillaries, maxillaries and frontals. Also fused to the nasals (or perhaps an outgrowth of the nasals) is the nasal horn core. The latter is the most conspicuous feature of the snout after the prominent rostral beak. In lateral profile the nasal horn forms a forward projecting wedge of about 60 degrees. Its forward inclination is also ab-

out 60 degrees from the "horizontal" (= the axis of the inferior maxillary margin). The nasal horn core is not completely preserved, the apex (approximately 7–10 cm) is missing. Also, the horn has been split along its axis by a fracture that separates the anterior and posterior halves, thereby giving the horn a much broader and more robust appearance in lateral view. Hatcher (1907) interprets this as a suture, the horn being constructed of the nasals behind and the premaxillaries in front. Our interpretation of this as a post-mortem fracture is evidenced by the distortion between the left and right sides of the snout. But additional support lies in the fact that no other sutures in the skull are open and most have become so solidly fused that their traces cannot even be located. It seems out of the question that the only remaining open suture would traverse one of the cranial horns!

Where natural surfaces are preserved, they appear rugose, but clearly defined vascular channels are not readily discerned. Behind the horn core, the nasals form a broadly convex bridge leading back to the frontals and prefrontals.

Frontal. As with the preceding elements, no sutures defining the frontal can be recognized. On the basis of other *Triceratops* specimens, this bone is presumed to support the prominent brow horn as well as forming the robust anterior and superior orbital margins. These latter are conspicuously rugose, forming substantial protection for the eye. The brow horns are broadly based and set directly above and behind the orbits. They have a slightly compressed oval cross-section throughout their length. They taper uniformly and are nearly straight in lateral and anterior aspect, pointing up and forward at approximately 50 degrees to the maxillary lower margin. Their surfaces are rugose, marked with numerous linear vascular channels many of which exit from distinct foramina. The frontal surface between the horns is concave, not rugose but feature fine bony trabecular patterns rather than vascular channels.

Postfrontal. The skull region usually formed by the postfrontal is broadly convex with no evidence of any sutures. No vascular impressions are preserved, but what has been interpreted as a nearly circular postfrontal fontanelle (ca. 5 cm in diameter) is situated in the mid-line immediately behind the brow horn bases. No other significant features are preserved here.

Jugal. As in all ceratopsids, the jugal here forms a prominent ventral flange or projection that descends from the posterior extension of the maxillary lateral shelf or overhang. This lies lateral to the quadrate and gives the impression of a bucklar or lateral shield protecting the jaw joint. The element is moderately robust, tapering (in lateral view) rather than parallel sided as in some species, and is marked by a very modest midwidth linear convexity; it cannot be described as a ridge as in other forms. The external surface is rough in texture with what may be described as vascular markings. The exact shape of the jugal cannot be determined here because of closure of all of the sutures, nor can a distinct epijugal be distinguished. Dorsal to the ventral jugal projection is a small (ca. 10.5×7.5 cm) lateral temporal fenestra, well-defined by robust rounded margins formed by the jugal below and the squamosal below, behind and above. Its long axis is inclined fore-aft at approximately 30 degrees to the horizontal.

Quadratojugal. This element cannot be recognized in this specimen. Presumably it is situated between the quadrate and the overlapping jugal projection.

Lachrymal. Marsh illustrated a distinct lachrymal in several other specimens of *Triceratops* (*T. prorsus*, *T. serratus*) but Hatcher did not so define the lachrymal in the present specimen. We are not able to define it either as all sutures in the lachrymal, prefrontal, jugal, maxilla region are completely obscured by fusion.

Prefrontal. As with the preceding element, a distinct prefrontal was illustrated in *T. prorsus* and *T. serratus* in the 1907 Hatcher, Marsh, Lull monograph, but no such delineation was shown for *T. brevicornis*. The very rugose swollen "eyebrow" like dorso-anterior rim of the orbits may well represent the prefrontal. The orbital rim below this "swelling" is much less swollen and forms a thinner-edged anterior and ventral rim of the orbit – perhaps reflecting contributions of the lachrymal and jugal to the orbital margin. Thus the swollen part of the orbit margin is distinctly set off from the rest, and might be a separate center of ossification – perhaps the prefrontal. That same region clearly serves as a buttress to the base of the brow horn in front. The need for such buttressing, and the swollen upper orbital rim is obvious.

Squamosal. This element forms the lateral third approximately of the posterior cranial crest or frill. It produces the laterally facing or flanking portion posterior to the lateral temporal fenestra. Sutures defining it are discernible on the right side leading from the lower margin of that fenestra to the lower lateral frill margin. Also, an apparent suture extends back from the upper apex of the temporal fenestra, but it is obscured on the frill upper surface. Presumably, this suture turned medially and extended to the supratemporal fenestra, as in most other adequately preserved ceratopsians, but that cannot be confirmed in the present specimen. Also, it is presumed on the basis of other specimens, that the squamosal extended back to the rear margin of the frill, but this is not verifiable. If correct, the squamosal length would be about 72 cm. The external surface is rugose and marked by irregular grooves and trabecular textures. The latter is especially evident behind and below the orbit. The under surface margins of the squamosal, where adequately preserved, display a peculiar "hummocky" polygonal pattern that almost certainly results from extensive fracturing of this broad bony plate. Elsewhere the under surfaces are smooth with finely textured vascular channels.

Parietal. Again, the lack of recognizable sutures precludes precise definition of this element. On the basis of younger specimens previously referred to other species of *Triceratops*, we may conclude that the parietals here form the median third or more of the posterior crest, extending from near the rear base of the brow horns (postfrontal area) and the possible postfrontal "fontanelle", to the rear margin of the crest. Both supratemporal fenestra are poorly preserved, thereby providing lateral landmarks delineating the approximate cranial proportions of the parietals vs squamosals – or roughly half each. The upper parietal surface is quite rough, marked with the same peculiar polygonal irregularities mentioned before that probably reflect multiple fractures (repaired) superimposed

on the original irregular pattern of vascular channels. The united parietals are moderately convex transversely and slightly concave longitudinally, producing an elevated fan-like crest. The parietal mid-line is slightly elevated near mid-length, but there is no evidence of the mid-line prominences described by Marsh in *T. serratus*.

Today, it is generally agreed that the median part of the ceratopsian frill is formed by the fused parietals, as described above. That was the original interpretation by Marsh, Hatcher and Lull in their early works. However, Hay (1908) argued that could not be so and suggested that the middle part of the frill might be formed by fused supratemporals or "nuchal" bones. Huene (1911) followed with the conclusion that the parietals formed the anterior part of the frill mid-region but the posterior part was constructed of the dermosupraoccipital. In 1914, Brown decided that the median part of the frill was formed by expanded and fused postfrontals, but Gilmore (1914) demonstrated that in *Brachyceratops*, the postfrontals do not extend back to form any part of the frill. Gilmore did, however, conclude that the parietals were not exposed on the dorsal frill surface and that that region was formed by a dermosupraoccipital in *Brachyceratops*. In 1919, Gilmore presented new studies of additional ceratopsian skull material (U.S.N.M. 5740 and 6679), which he referred to *Triceratops* sp. There he attempted to show that the parietal extended posteriorly and upward as a thin sheet of bone that underlapped what he called the dermosupraoccipital. It now appears that all this uncertainty about the construction of the ceratopsian frill derived from the highly fused state of frill components and fractures mistakenly identified as sutures. The question was resolved by the remarkable growth series of *Protoceratops* which clearly shows the gradual development of the frill by backward growth of fused parietals (Brown and Schlaikjer, 1940).

Epoccipitals. The lateral and posterior margins of the squamosals and parietals are preserved only in a few places where they show a "scalloped" edge that is suggestive of the epoccipital bones preserved in other specimens. However, these crest-edge features appear to be continuous (fused with?) the squamosal or parietal and cannot be recognized as distinct or separate ossifications. In shape they appear to have been very broad and low obtuse triangles, the obtuse apex pointing out away from the frill edge.

Quadrate. Except for the anterior surface of the distal end, the quadrate is visible only in its posterior aspect. Viewed from behind, it forms a stout shaft, transversely expanded, that ascends with a slight backward pitch to contact the reinforced antero-inferior region of the squamosal just anterior to the robust transverse process of the exoccipital. Partially exposed is the pterygoid flange of the quadrate extending medially and only slightly forward to contact the pterygoid (not visible). The distal quadrate extremity is not complete on either side, but in other *Triceratops* specimens the transversely expanded shaft terminates in a robust "double condyle" – with distinct inner and outer condyles separated by a broad trough or trochlea for articulation with the mandible. The junction between the quadrate and squamosal is not visible.

Exoccipital. This robust bone extends laterally from the occipital condyle and foramen magnum as a stout oval-section shaft approximately 5 cm in vertical diameter. This fans out into a broad dorso-ventral buttress that contacts the ventral surface of the anterior part of the squamosal. This structure appears to be the primary support of the entire frill forming a solid union at the crest base with the junction of the quadrate and squamosal. These transverse braces extend approximately 30 cm on either side of the mid-line, or about half the maximum width of the expanding frill behind. No sutures between this and the adjacent occipital elements are detectable.

Supraoccipital. The region above the foramen magnum is not well enough preserved to describe any details other than to note that there are two very deep depressions (ca. 4×7 cm) close to the mid-line (where they are separated by a thin vertical lamina of bone) and about 4 to 5 cm above the foramen. These are set at the bottom of a larger triangular mid-line depression about 14×18 cm. Presumably these features are related to the cranial attachments of what must have been an enormous ligamentum nuchae and powerful M. spi-

nalis capitis. On either side of this region lie two basin-like depressions (ca. 10×15 cm) situated dorsal to the exoccipital braces, that probably were the sites of attachment of the M. obliquus capitis magnus and M. transversalis capitis. These large concavities presumably are floored by the parietals, but that cannot be established.

Basioccipital. Although no sutures are visible here either, the nearly spherical occipital condyle, standard equipment in all ceratopsians, is well preserved here. It has a transverse diameter of 8.8 cm and a vertical dimension of about 8.0 cm. This is about three times that of the foramen magnum that measures 3.0×3.5 cm. The condyle projects slightly downward at about $30\text{--}35$ degrees relative to the "horizontal" datum adopted here (inferior margin of the maxilla). Undoubtedly this reflects the linear "axis" of the cervical series and thus is a clear indication that the head was carried in a "pitched forward" attitude — a nose down position (see Fig. 7).

Pterygoid, Vomer, Ectopterygoid, Basisphenoid, Laterosphenoid, Palatine, Prootic. None of these bones are visible here.

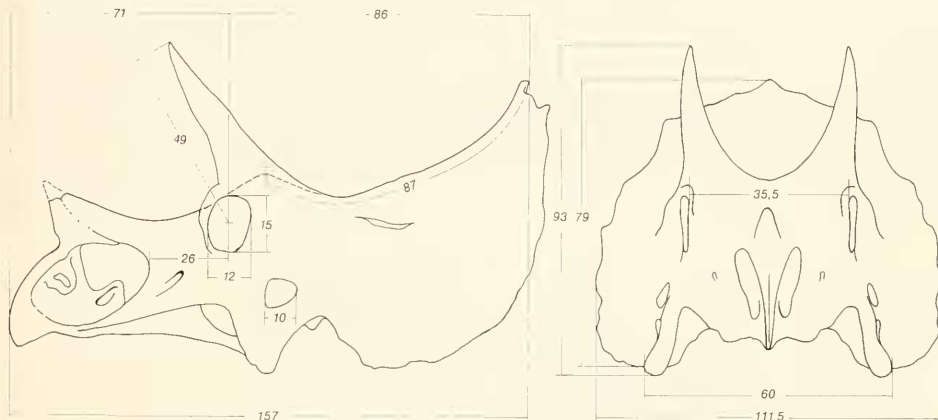


Fig. 4: Measurements (in cm) of the skull of type specimen of *Triceratops "brevicornus"*.

Mandible

The lower jaw, very massive and robust, is composed of a long and wide dentary with a stout coronoid process, a sturdy median predentary and part of the surangular. The posterior parts of the mandible are not preserved here, the angular, prearticular and articular are missing so that nothing can be said about the morphology of the glenoid or the retroarticular process. The splenial also is either missing or cannot be identified here. The two massive rami diverge widely from their anterior union with the predentary. The preserved angle is distorted, but the original divergence must have approximated 20 degrees or more if the present form of the predentary is any indication. The dentaries supported long (ca. 35 cm) dental batteries that extended almost the full length of that

bone. The wedge-shaped predentary beak is a robust median element that unites the two dentaries anteriorly, probably in a rigid junction. The extent of inter-dentary contact at the symphysis cannot be measured, but it appears to have been significant. The overall preserved length of the mandible to the end of the surangular is 74 cm. The retroarticular process must have added approximately 6 to 8 cm more. The massive and robust construction of the lower jaws undoubtedly is related to the large dental batteries, their heavy use as exclusively shearing structures, and the powerful jaw musculature that powered the peculiar masticating apparatus of ceratopsians.

Dentary. The largest bone of the mandible by far, the dentary constitutes close to two thirds of the total jaw length. Anteriorly, it forms a moderately thick, nearly vertical plate

of bone convex laterally and strongly concave medially. Posteriorly, the medial concavity diminishes as the dentary expands transversely. At mid-length both the inner and outer surfaces are strongly convex housing the unerrupted replacement teeth of the dentary battery. Also at about midlength, the lateral surface of the dentary expands outward into a longitudinal ridge which flares out posteriorly into the base of the coronoid process. This process expands out and upward into a very thick (transversely) dorsal projection that rises well above (ca. 10 cm) the dentition lying medial to it. Dorsally, the coronoid process expands antero-posteriorly forming

a large spatulate extremity. Undoubtedly this robust process served as a critical attachment site for powerful adductor muscles — most likely the *M. pseudotemporalis* and the deep portions of the *M. adductor externus* (Lull, 1908; Ostrom, 1964). These muscles must have attached here by powerful tendons that passed up through the supratemporal fenestra to large muscle masses originating on the frill dorsal surface. A distinctive aspect of the coronoid process is its extreme lateral position relative to the dental battery and the main body of the dentary — a position 8 cm lateral to the tooth row.

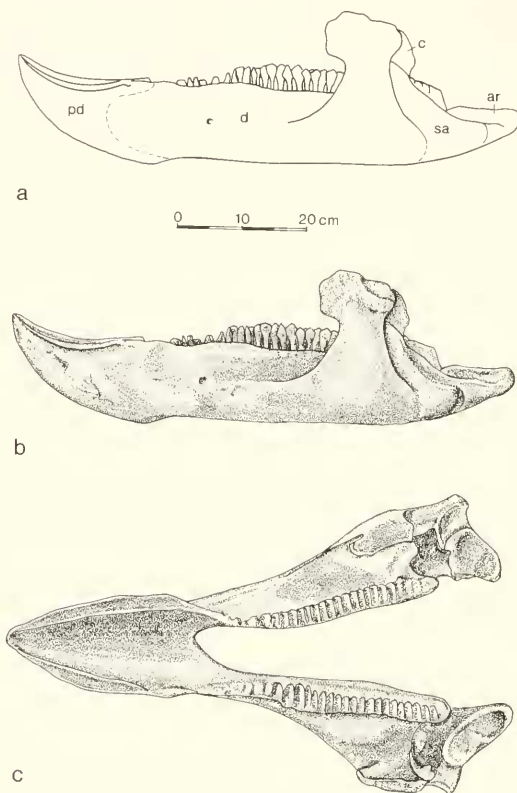


Fig. 5: Mandible of type specimen of *Triceratops "brevicornus"* with jaw elements indicated as follows: ar articular, c coronoid, d dentary, pd prearticular, sa surangular, in left lateral view (a, b) and in dorsal view (c).

Neither dental battery is preserved intact, but the left battery is nearly complete and is the most informative. Its original length was not less than 35 cm and it consists of 21 preserved functional teeth, plus another 5 tooth positions where one remain. (There may have been one or two more tooth positions that are no longer evident in this specimen.) The teeth are enameled lingually and feature a prominent vertical keel that bisects the medially facing crown. Dentary teeth erupt-

ted up and outward in order to maintain maximum occlusal shear against the upper battery teeth that were enameled laterally and erupted downward and inward. The tight fore-aft compaction along the tooth rows insured uninterrupted dental blades as alternate tooth positions replacing worn teeth were filled by the expanded crowns of the functioning teeth in front and behind (see Fig. 5).

The medial surface of the dentary is marked by a prominent horizontal row of large round foramina, each one of which seems to correspond with a tooth position, as in the hadrosaurs. These have been interpreted as nutrient canals, but Brown and Schlaikjer (1940) dismissed this and argued that they provided for the passage of branches of the mandibular nerve, as similar foramina do in modern crocodilians. But they also suggested that these openings resulted from bone adsorption at the base of each tooth series. Edmund (1957, 1960) demonstrated that these foramina almost certainly served as passages for migration of germ teeth from the dental lamina to the alveolar sites during the life-long cyclical tooth replacement phenomenon in these ornithischians.

At the base of the coronoid process facing posteriorly is the large adductor fossa which leads forward into the Meckelian canal. The opening to this fossa is bordered by the dentary medially and anteriorly (the base of the coronoid process) and surangular laterally. Posteriorly, it presumably is bounded by the prearticular, which is present here as only a small fragment at the rear of the surangular. Much of the adductor fossa lies within the base of the coronoid process and served as the major insertional site for the M. adductor posterior; its size is a good indication of a very large adductor muscle.

Predentary. As in all ornithischians, *Triceratops* is characterized by a median, unpaired predentary bone. This element has the form of a pointed, wedge-shaped trough – not unlike a garden trowel. The tip probably was relatively sharp in life and the upper edges of the enclosing horny beak almost certainly were sharp-edged. The upper edges of the predentary, however, are broad with distinct longitudinal grooves or channels from 1 to 2.5 cm in width. Presumably these

marginal grooves served as a firm foundation supporting a much sharper-edged horny beak that ensheathed the entire predentary. Presence of such a beak is indicated by the lateral surfaces which are rugose and are marked by vascular channels and foramina. The inner surface seems to have had similar texture but very much subdued. It cannot be determined in this specimen whether or not there was a median posterior process that intruded between the left and right dentaries at the symphysis. However, the exterior surface clearly shows a posterior projection in the ventral region. Similarly, there are posterior projections that overlap the dorsal margins of both dentaries – forming the rear extremities of the grooved upper margins of the predentary. Needless to say, the predentary is edentulous.

Surangular. This element is partially preserved on the right side. It articulates with the posterior external part of the dentary as a buttress to the posterior margin of the coronoid process. It is concave medially where it forms the lateral wall of the posterior part of the adductor fossa. Laterally, it is convex, grading into a dorsal ridge lateral to the fragment of the prearticular. As noted earlier, the angular cannot be recognized, but presumably it was situated directly below the surangular in its normal position at the inferior posterior extremity of the dentary.

Coronoid? A thin, irregular-shaped plate of bone has been attached to the upper rear margin of the left coronoid process. Its edges are incomplete, and at first glance it appears to be anomalous. No such feature is present on the right side, so at first we considered this to be a mistaken placement of a fragment of bone – except there was a written message on the fragment: “-nd just below left dentary 22”. The number refers

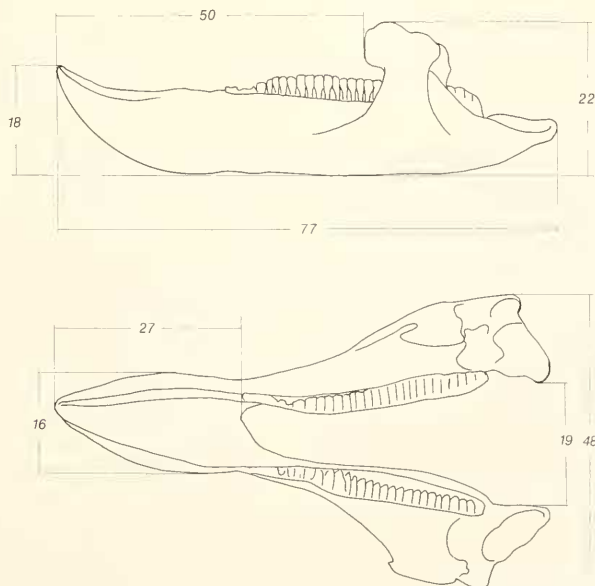


Fig. 6: Measurements (in cm) of the mandible of type specimen of *Triceratops* “*brevicornus*”.

to 'skull 22', which is Hatcher's field number for this specimen. The fragment fits perfectly against the coronoid process and comparison with figures 10 and 11 in Brown and Schlaikjer (1940) of the mandible of *T. sulcatus* (A.M.N.H. 4276) confirm that this fragment must be the accessory coronoid bone. Of special interest is the fact that the junction between the coronoid and the coronoid process of the dentary is an open suture. The right coronoid process shows a finished articular surface for the missing right coronoid. In as much as the coronoid process was the point of attachment of the main adductor jaw muscles, we would expect the union of these two bones to have been firm and any suture completely obliterated by fusion.

Angular, Articular, Prearticular, Splenial. These jaw elements are either missing, or not discernible in this specimen.

DESCRIPTION OF POST-CRANIAL MATERIAL

To the type skull belongs a complete series of presacral vertebrae, one complete anterior caudal vertebra, a number of cervical and dorsal ribs and rib fragments, numerous fragments of ossified tendons originally attached to the neural spines of the dorsals, the right pubis and a fragmentary part of the ilium blade. Additionally are many unidentified bone fragments.

Axial Skeleton

Originally the presacral vertebral column was embedded in a sandstone concretion, exposed and prepared from its left side. The vertebrae were in their natural articulation as figured by Hatcher (1907, fig. 48, pl. 40, fig. 1). Only after the transfer to the Munich State Collection were the vertebrae prepared completely out of the matrix and restored by the preparator Leonhard Bimmer under the supervision of the junior author (P.W.) in 1982 and 1983, more than ninety years after its discovery.

There has been disagreement between R.S. Lull and J.B. Hatcher as to the number of cervicals (in Hatcher 1907:46). Lull referred to the specimen of *Triceratops prorsus* Marsh (Y.P.M. 1822), where he believed he could recognize "a distinct suture seen 3 to 4 mm (sic, 3–4 cm) behind the anterior margin of the atlas . . . , indicating that the so-called atlas of Hatcher's above description is in reality the atlas and axis, while the axis of Hatcher represents the third, and the third = the fourth cervical. The atlas is therefore reduced to a ring-like bone of somewhat greater fore and aft extent inferiorly than towards its side." (Footnote of R.S. Lull in Hatcher 1907, p. 47). Based on these different views the number of the cervicals is given as 7 (Hatcher) and 8 (Lull) respectively.

The anterior cervicals are coossified in the genus *Triceratops*, and in *Monodinus* and has been reported in other ceratopsians as well. From the material of *Triceratops brevicornis* it is not clear, whether the first four or the first three cervicals are fused. A suture as indicated by Lull in *Triceratops prorsus* is not recognizable here, but the anterior-most part of the coossified cervical section is not quite complete and has been

partially restored. In any case, the atlas could not have been a ring-like bone as suggested by Lull, because the anterior cavity for the reception of the ball-like occipital condyle is formed by continuous bone from the margin of the cup-like cavity to its deepest point, about 4 cm from its sharp anterior margin, which is almost circular in outline.

If we follow Hatcher, then the first three cervicals were coossified. In this case the atlas would have featured a large neural arch terminating in a massive posteriorly directed neural spine, forming a united structure with the neural spine of the following cervical. Since this would be a quite unusual condition, we think that the atlas-axis is a completely fused complex in which no distinction between the two elements is possible and no sutures can be observed. We agree therefore with Lull taking cervicals one to four as elements of the coossified complex (which could be called syncervicals), and thus a total count of eight cervicals.

Some uncertainty remains about the division between the cervical and dorsal series. As stated by Hatcher (1907:47), it "is indicated not so much by differences in the vertebrae themselves as by the differences in the ribs which they support." The series of the cervical ribs preserved in *Triceratops brevicornis* is fairly complete. The ribs of the atlas-axis complex are not preserved, but must have been present. The rib of the eighth vertebra is clearly a typical straight cervical rib. None of the dorsal ribs and rib fragments preserved can be assigned to the ninth vertebra. Only the following vertebra, which in our count would be the tenth, has a long rib which obviously is a dorsal rib with a strong lateral curvature. The transverse processes of the ninth vertebra, however, show large articular facets for the tuberculum costae, indicating the presence of a large rib which in all probability was the first dorsal rib.

Cervical Vertebrae (Plates 2 and 3)

Cervicals 1 to 4: As above stated, there are 8 cervicals, the first four being a solid coossified complex ("syncervicals"). No sutures can be determined between the four elements, nor can there be separated single elements of the atlas and axis. The neural spines of the axis and the third cervical are fused as well, closely attached to and lying above the neural spine of the fourth cervical, sloping backward and upward. The neural spine of cervical 2+3 ends in a lateral expansion while it is laterally compressed in the middle with a relatively sharp dorsal ridge. The neural arch of cervical four is more robust and more elevated and strongly expanded transversely at its summit.

The postzygapophyses of the fourth cervical have oval, flat articulation surfaces forming an angle of 70° converging ventrally. The neural canal of the fourth cervical is at its exit somewhat triangular in outline. It is 37 mm wide and about 45 mm high. Short and blunt transverse processes project laterally at the neural arch of that vertebra, terminating in a diapophysis for articulation with the cervical rib. The corresponding parapophysis appears as a strong projection situated anterolaterally at the centrum and below the rib of the third cervical which is fixed in its natural position.

Lateroventrally there are deep cavities in the centra of cervicals three and four. A circular foramen beneath the coossified neural spines of cervicals two and three as described by Hatcher (1907:48) as passing "quite through from one side to the other" could have been present but is filled here by matrix. The cup-like anterior articular surface of the atlas/axis complex is deeply excavated for the reception of the occipital condyle. It is almost circular in outline with a diameter of about 100 mm and a maximum depth of 40 mm. The posterior articular surface of the coossified four cervicals is strongly concave reaching a maximum depth of more than 20 mm. The fourth cervical is wider than high at its posterior end.

Cervical 5: This is the first free cervical. The vertebra is amphicoelous as is true for all vertebra of *Triceratops*. The articular ends of the centrum are almost circular in outline, though slightly wider than high. Laterally, the body of the centrum is strongly concave except for two longitudinal ridges parallel to the ventral mid line and lateral rounded elevations dividing the side of the centrum into superior and inferior concavities. The parapophysis is a strong projection of this elevation near the anterior margin of the centrum. The neural canal is circular in outline with a diameter of about 42 mm. The transverse processes extend laterally and are directed slightly upward. The diapophyseal articulations are not completely preserved. In cross section the transverse processes are flattened. The prezygapophyses are much produced and overhang the centrum anteriorly. Their oval, almost flat articular surfaces point inward and upward. The postzygapophyses are situated well up on the posterior sides of the neural spine, and do not overhang the centrum. Their articular surfaces enclose an angle of 90°. Between the postzygapophyses a deep groove rises from the roof of the neural canal about half way up the posterior side of the neural spine with scars of the interspinous ligaments. The neural spine is more upright as in the preceding vertebra with a more inclined anterior margin and an almost vertical posterior margin with a posterior projection at the top. The upper extremity of the neural arch is thickened transversely.

Cervicals 6 to 8: The last three cervicals are similar in shape and size with gradually increasing total height. Compared to the fifth cervical the transverse processes become stronger, tending more upward rather than transversely. The width of the centrum decreases relatively to the height with a tendency to a more oval outline as is typical for the following dorsals. The neural spines of these cervicals are more vertical than in the fifth cervical, but in comparison to the dorsals still relatively low. The neural spines of cervicals 6 and 7 are expanded at their upper extremities, whereas cervical 8 has no expansion at all. The diapophyses have relatively small articulation surfaces for the tuberculum of the ribs. The parapophyses are circular depressions set off the upper half of the side of the centrum. They keep this position throughout the cervical series.

Dorsal Vertebrae (Plates 4–10)

There are 14 dorsals preserved. It can not be determined whether the last preserved dorsal is the vertebra in front of the first sacral. If so, then there would be no lumbar (as noted by

Marsh, 1891b) and the last dorsal would have supported a double-headed rib.

Dorsal 1: The first dorsal has a considerably higher neural spine than the last cervical. The transverse processes are much stronger and longer, and point upward almost at an angle of 45°. Their cross-section is more triangular. The articular facet for the tuberculum of the rib is large and faces laterally. The parapophysis is higher up on the centrum as in the last cervical. The posterior margin at the extremity of the neural spine is expanded, whereas the front edge is sharp. As in all other dorsals the centrum is deeply excavated laterally. The articular surfaces are biconcave. The zygapophyses are robust and their articular facets are flat and face downward and outward (postzygapophyses) and upward and inward (prezygapophyses) respectively.

Dorsal 2: The second dorsal has the same general characters as the first dorsal, but the neural arch is considerably higher, the transverse processes are even more robust and longer, and the centrum is more oval with the long axis being vertical. The parapophysis is situated in a similar position on the centrum as in the first dorsal. Ventral to the postzygapophyses the neural arch is deeply excavated for the reception of the prezygapophyses of the succeeding vertebra.

Dorsal 3: The trend shown in the preceding dorsal continues in the third dorsal, with the transverse processes rising still higher, but also backward, overhanging the centrum. The main difference lies in the position of the capitular rib facet which has moved up from the side of the centrum to the base of the neural arch and above the level of the top of the neural canal. The parapophyses face upward and outward as is the case with the diapophyses, too. The neural spine is more posteriorly inclined than the almost upright neural spine of the second dorsal. Posteriorly there are two deep excavations underneath the postzygapophyses separated by a sharp medial crest running down to the upper border of the neural canal.

Dorsals 4 to 14: The morphology of these vertebrae is so similar that a general description would at first apply to all the succeeding dorsals. The centra are oval in cross-section, the neural arches are very high except the posterior dorsals. This can be shown in the fourth through the seventh dorsal and may be true for the following ones, although the centra of the eighth through the fourteenth dorsal are not preserved. The parapophysis gradually moves up from the side of the neural arch to the ventral surface of the transverse process which is reached in about the sixth or seventh dorsal. Towards the posterior end of the series the diapophysis and the parapophysis approach each other. This is partly due to the fact that the transverse processes decrease in length towards the end of the series. At the same time they become somewhat weaker. The most striking change from the anterior to the posterior dorsals is shown by the position of the zygapophyseal articular facets. In the first dorsal these facets form an angle of 70° which gradually increases in the succeeding dorsals until an angle of about 180° in the 14th dorsal (see also table of measurements). The neural arches become broader from the sixth dorsal on. The neural arch is highest in the seventh through the ninth dorsal. The mid dorsals also exhibit the strongest

transverse processes, triangular in cross-section. They overhang the posterior end of the centrum much more than in the anterior or posterior dorsals.

Caudal Vertebrae
(Plate 10)

One more or less complete caudal is preserved. According to the caudal of *Triceratops prorsus*, figured by Hatcher 1907 (Fig. 58), it can be assigned to the mid caudal series. The amphicoelous centrum is broader than wide. There is a cavity on

its ventral surface. The transverse processes have their origin at the sides of the centrum. They are directed laterally at right angles to the centrum. The neural arch is still higher than the centrum. A strong neural spine with a thick expansion at the top is strongly inclined backward overhanging the centrum. On its posterior side two short postzygapophyses are developed facing outward and downward at an angle of about 75°. This corresponds to the prezygapophyses projecting upward and slightly outward with their articular facets facing upward and inward. The neural canal is filled with matrix. Its diameter might be about 15 mm.

TABLE 2: MEASUREMENTS OF VERTEBRAE OF THE HOLOTYPE OF
TRICERATOPS "BREVICORNUS" (in mm)

Vertebra	Length of centrum	Height of centrum	Width of centrum	Total height of vertebra	Width over transverse processes	Height of neural arch above bottom of neural canal	Angle of zygapophyseal articular facets
Cervicals 1-4 (coossified)	360	--	--	--	--	--	--
Atlas/Axis	--	122	109	--	--	--	--
Cervical 3	--	--	--	256	--	--	--
Cervical 4	--	122	143	272	146	145	70°
Cervical 5	90	125	145	304	220*	174	90°
Cervical 6	85	128	132	315	208*	180	85°
Cervical 7	85	124	128	316	240	192	63°
Cervical 8	80	128	124	320	?	192	78°
Dorsal 1	84	120	120	352	248	216	70°
Dorsal 2	84	128	124	380	256	252	90°
Dorsal 3	84	132	108	408	256	276	95°
Dorsal 4	84	132	104	420	256	284	108°
Dorsal 5	88	140	100	440	280	300	106°
Dorsal 6	96	140	ca. 88	444	268	304	130°
Dorsal 7	92	124	96	436	280	312	140°
Dorsal 8	--	--	--	--	268	312	150°
Dorsal 9	--	--	--	--	260	312	ca. 150°
Dorsal 10	--	--	--	--	256	ca. 305	ca. 150°
Dorsal 11	--	--	--	--	264	--	ca. 160°
Dorsal 12	--	--	--	--	272	ca. 300	ca. 170°
Dorsal 13	--	--	--	--	248	--	ca. 175°
Dorsal 14	--	--	--	--	--	--	ca. 180°
Caudal	60	80	ca. 90	200	ca. 240	ca. 120	75°

* restored

Functional Significance of the Vertebral Column
(Figure 7)

The first four cervicals are coossified in *Triceratops brevicornus*, and form a solid block of vertebrae. The anterior articular facet of this complex forms a deep circular socket for the articulation with the ball-like occipital condyle, thus providing a wide range of free movements of the head. The mobility within the vertebral series was controlled by the zygapo-

physeal articulations. In these, however, there are considerable differences between the anterior and the posterior presacral vertebrae. The angle formed by the articular facets of the zygapophyses is rather steep in the anterior cervicals, becoming gradually less inclined towards the posterior vertebrae (table 2). The zygapophyseal angle in the fourth cervical is 70°. With some variation it reaches 90° in the second dorsal, 150° in the eighth, and finally about 180° in the fourteenth and last preserved dorsal.

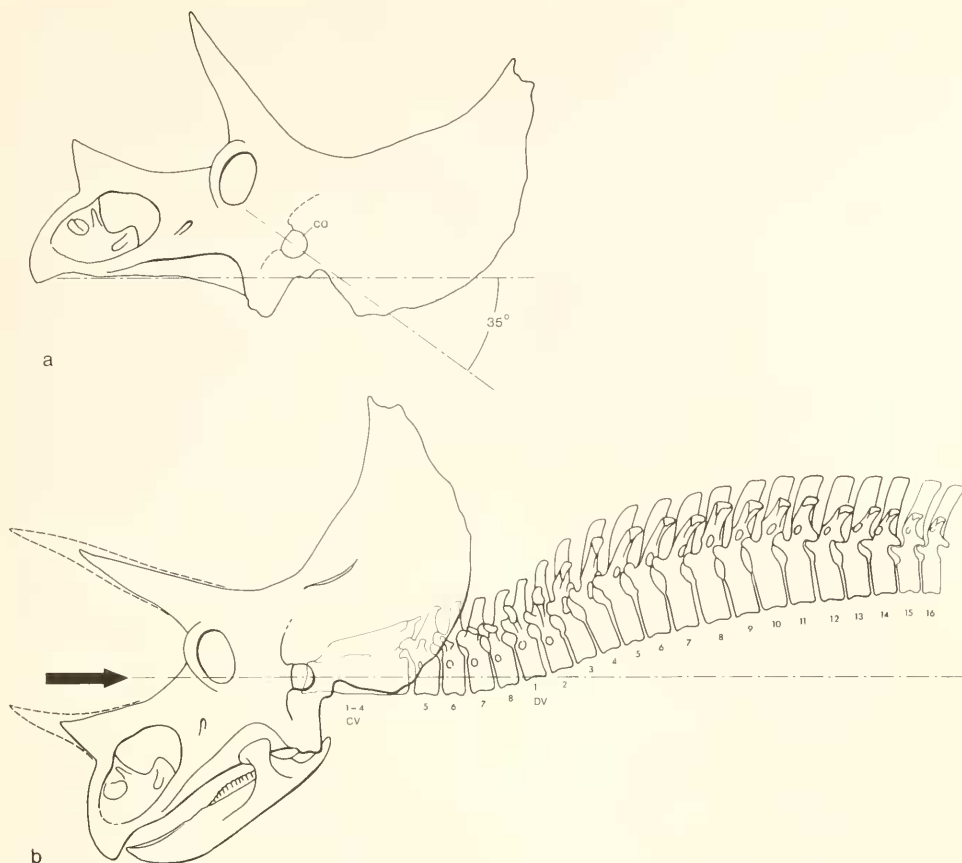


Fig. 7: (a) Skull of *Triceratops* in lateral view showing the position of the occipital condyle (co) pointing posteroventrally relative to a datum line parallel to the inferior margin of the maxilla. — (b) Skull of *Triceratops* in articulation with the vertebral column. The head is lowered, so that the long axis of the occipital condyle is horizontal. In this suggested aggressive pose the force of impact travelled through the condyle and the coossified solid block of the syncervicals (1–4), and was successively transmitted through the slightly curved vertebral column, thus absorbing the shock. The actual brow and nasal horns were probably extended to meet a vertical plane in this attitude simultaneously. So, a collision with an aggressor must have been most effective. The arrow indicates the direction of the force of impact. CV: Cervical vertebrae, DV: Dorsal vertebrae.

Due to the steep attitude of the zygapophyseal facets in the cervicals and anterior dorsals, the degree of lateral mobility of this region of the vertebral column was much more limited than was dorsoventral movement. In the middle and posterior series of dorsals the more horizontal arrangement of the zygapophyseal joints allowed greater lateral movement compared to dorsoventral flexion – extension.

The fact that the anterior limbs of *Triceratops* are considerably shorter than the hind limbs results in a downward curvature of the neck and anterior dorsals. Feeding activities required up and down mobility in this section. The limitations of lateral neck and anterior trunk movements probably correlate with the way the horns were used for attack or defense.

The occipital condyle points posteroventrally at an angle of 30° to 35° relative to a horizontal datum line defined by the lower edge of the upper jaw. When *Triceratops* took his defensive pose, the most effective and least injurious orientation of the head would align the longitudinal axis of the occipital condyle to coincide with the expected impact forces. That axis was brought into horizontal orientation by lowering the head. In this position both the nasal horn and the brow horns point forward, and the neck frill is raised to a more upright position thus directing the horns against the aggressor and displaying the head shield. When attacking the impact forces were transmitted through the occipital condyle to the complex of the four coossified cervicals oriented horizontally.

The restricted lateral mobility of the cervicals prevented bending the neck to either side and strengthened the structural axis between the cranial armature and the trunk and legs.

The morphology of the presacral vertebrae was clearly related to actions of defensive behaviour, but it must also have been related to the mode of feeding and locomotion. As was shown, up and down movements in the posterior dorsal series was restricted while transverse flexion was enhanced. Whether Ceratopsians had a cursorial ability similar to that of a modern rhinoceros as was suggested by Bakker (1968), we don't know. Examination of the vertebrae of *Triceratops brevicornis* seems to indicate a rather stiff-back mode of walking and an elephant-like running gait, but not a high speed gallop. The analysis of the limbs given by Coombs (1978) suggests poorer running ability in the ceratopsians, too. According to this author ceratopsians were low-grade to intermediate grade mediportal animals, similar to or slightly better than *Hippopotamus* in cursorial ability.

The Ribs (Plate 11–12)

Cervical Ribs. No ribs of the atlas/axis-complex are preserved. A tubercular projection at the right side of the centrum of the axis is present indicating an axial rib. The third cervical rib is still connected with the third cervical vertebra. It is double-headed as are the succeeding ribs and is articulated to a pronounced diapophysis and parapophysis, situated laterally on the centrum. The position of the parapophysis is more antero-ventrally. Both the left and right ribs of the fourth cervical are preserved. The tuberculum was anchored to a short and stout transverse process projecting laterally from the base of the neural spine. The caputular ramus of this rib is much longer than the tubercular branch and is situated ventrally and anterior to the diapophysis. The rib is short, straight and triangular. Its medial surface is concave. The fifth cervical rib is more arched than the preceeding one. The tubercular branch appears to be weaker than the caputular. The rib is a flat bone pointed distally. The sixth cervical rib is more expanded in its middle part to a bony blade with a concave

medial surface. Distally it terminates in a short pointed tip. Along the longitudinal midline a low edge is developed. Above this edge the rib is somewhat flattened in order to let the preceeding rib overlap. Of the seventh rib only fragments are preserved. Obviously it had an intermediate size between the sixth and the eighth rib. This last cervical rib is a flat bone with a distal extremity longer than in the preceeding ribs. Both the caputulum and the tuberculum are widely branched and have oval articular facets.

Dorsal Ribs. The first dorsal rib is missing. Only the second through the sixth dorsal ribs are preserved although not complete. The caputulum of the second rib projects from the shaft almost at a right angle. In cross-section the shaft is oval and medially curved. In natural articulation with the second dorsal it points downward. Its distal end is broken away. The third dorsal rib is rather flattened proximally. The direction of the caputular ramus indicates that the rib pointed more ventro-laterally, rather than ventrally, a tendency which is gradually followed by the succeeding ribs. The fourth rib is only a little smaller, but it is broader, thinner and more blade-like. Of the fifth and sixth dorsal ribs only the articular section is preserved. They are similar to each other and considerably weaker than the anterior ribs. The caputulum forms a continuous extension of the shaft, the tuberculum projects only a little. This indicates that the posterior ribs become increasingly more laterally directed rather than ventrally.

The Pubis (Plate 11)

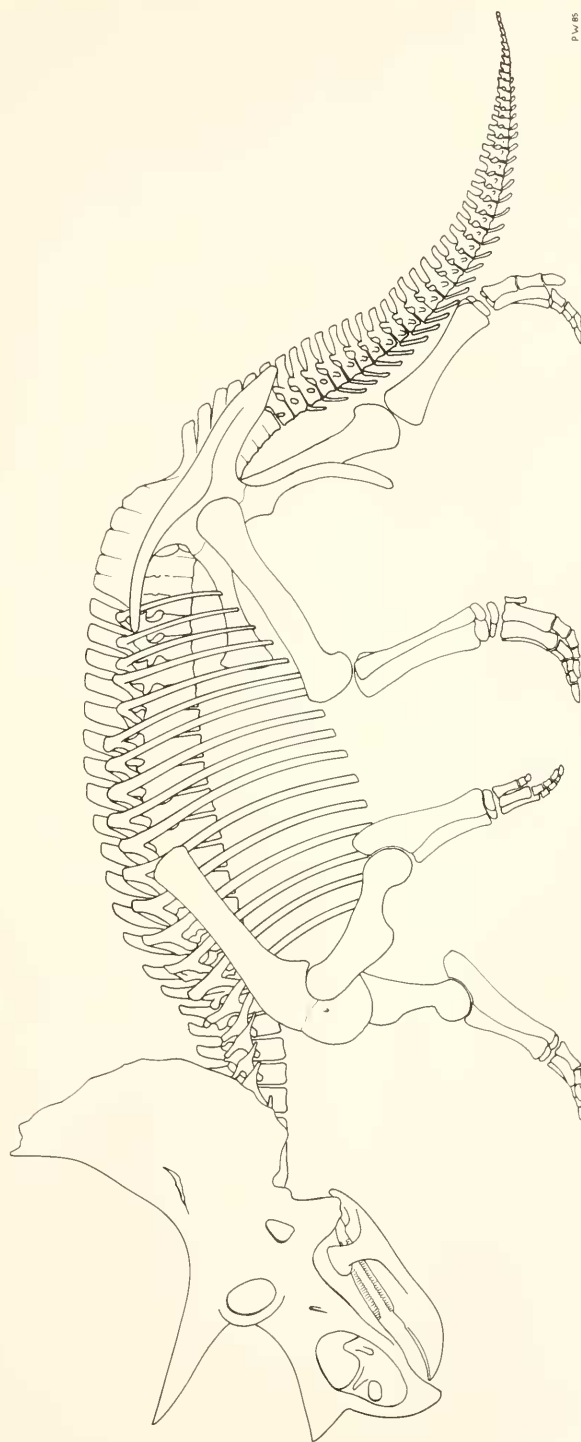
Except for the proximal portion, the right pubis is present. So, most of the postpubic process and the surface for contact with the ischium are missing, but here restored in plaster. The distal extremity becomes flattened and is expanded dorso-ventrally up to about 18 cm. The length of the pubis as restored was about 55 cm. Near the proximal end the remains of the anterior border of the acetabulum are preserved. In general, the shape of the pubis is very similar to the pubis figured by Hatcher 1907 (Fig. 62) assigned to *Triceratops prorsus*.

RESTORATION OF THE SKELETON OF *TRICERATOPS*

(Figure 8)

All skeletal restorations of *Triceratops* in the scientific and popular literature are duplicates of the restoration given by Marsh (1891 b). Marsh based his line drawing reconstruction on the *Triceratops prorsus* mount of U.S.N.M. 4842. According to Gilmore (1905) the most complete specimen was used as a basis for the mount. The missing parts were substituted from other individuals. No skull was preserved with specimen no. 4842. So, Skull no. 2100 was added to the postcranial skeleton. As already recognized by Gilmore, the number of presacral vertebrae was overestimated by Marsh. In the pre-

served presacral vertebral column of the type specimen of *T. brevicornis* Hatcher et al. (1907) recognized 21 presacrals, Lull in the same work 22, the difference being due to the presumption of three or four syncervicals respectively. It was suggested that the presacral series was complete in this specimen. There is no evidence for this, however. In our restoration we added two more presacrals resulting in a total count of 24 presacral vertebrae including 8 cervicals. This is in agreement with one of the most complete ceratopsian skeletons known, *Monoclonius nasicornus* Brown, A.M.N.H. 5351, a cast of



P.W. 85

Fig. 8: Restoration of the skeleton of *Triceratops* based on the type specimen of *T. "brevicornus"* (skull and presacral vertebrae, B.S.P. 1964 I.458) and on *T. "prosus"* (remaining postcranial elements, U.S.N.M. 4842, after Hatcher et al. 1907) reduced to the scale of the skull and the vertebrae. *Triceratops* is shown here in its defensive pose with the head carried in a "pitched forward" attitude (see fig. 7, p. 129). Total length eight meters.

which is on display in the Bavarian State Collections in Munich. This, however, is contradictory to Brown (1917) who counted only 21 presacrales.

For the appendicular skeleton we used in our restoration the proportions of *T. prorsus*, U.S.N.M. 4842, reduced in size to fit the vertebral column of B.S.P. 1964 I 458. The proportions could be double-checked with the pubes preserved in both specimens.

Although the restoration of *Triceratops* presented here is not founded upon a single individual, the skeletal proportions

seem to be closer to reality than the ones suggested by Marsh and Gilmore. Since in our opinion (see p. 156) *T. prorsus* and *T. brevicornus* should be regarded as synonyms of *T. horridus*, the components of the restored skeleton come from one species. Compared with Marsh's restoration the skull appears to be relatively bigger in our attempt. This in turn would mean that in the U.S.N.M. 4842 mount of *Triceratops* the skull is too small for the postcranial skeleton and comes from a smaller individual.

PART II: SYSTEMATICS OF *TRICERATOPS*

INTRODUCTION

A first step in our restudy of the Munich specimen was to confirm the distinctive nature of B.S.P. 1964 I 458 and to evaluate the specific designation. We were and are concerned about its separate taxonomic assignment. This led to re-examination of the bases for the designation of all of the other species of *Triceratops*. Very soon, we realized that our original project had broader and much more significant ramifications than we had anticipated. The result is a much expanded report in which we propose a radical systematic revision of the genus

Triceratops. In our opinion, the Niobrara County sample of ceratopsian specimens provides an unusual illustration and opportunity to address the issue of the species question in large extinct animals. It is perhaps the best assemblage available for such consideration and challenge.

This section deals with the historical and scientific data pertaining to *Triceratops*. It is an essential preface to Part III and our taxonomic conclusions.

THE NAMED SPECIES OF *TRICERATOPS*

Since its foundation in 1889, sixteen species have been named or referred to the genus *Triceratops*. In this section, all of these are discussed in the order in which they were proposed. The material on which each species was founded is summarized and the "diagnostic" characters for each are quoted, at least in part, or listed from the original citation. These are followed by relevant comments and description (not usually as diagnoses) by subsequent students. Of necessity, these anatomical details are lengthy, tedious and repetitious, but they are necessary here in order to understand the historical establishment of these taxa and the criteria applied by their authors. In reviewing these taxonomic statements it is important to recall the "state of the art" and the "philosophy" of taxonomy that prevailed late in the 19th century. The "type" concept was the rule of the day and little was understood about variation within populations, although variation must have been of some concern. It is also important to realize that in most instances, each new species was established in comparison with previously named species (few at first) and sometimes comparable characters were not available. The two monographic studies that followed were conscientious attempts to revise and recognize those ceratopsian taxa that were deemed most likely valid.

The present effort is concerned only with the genus *Triceratops*, the most speciose of all ceratopsians. This review was prompted initially by our desire to establish, in so far as possible, the validity of the Munich specimen as *Triceratops brevicornus*. That objective was reinforced by a nagging question that could not be dismissed: Is it really likely that the Colorado-Wyoming-Montana area was inhabited by the ten or more large species of *Triceratops* during the brief geologic span of Lancia time as reported? Does it seem reasonable that the restricted region that is now Niobrara County, Wyoming could possibly have sustained ten large and closely related species? Granted, these many "species" were not all recovered from the same stratigraphic horizon, but the Lance exposures (1300') do not span more than two million years (McKenna, personal communication), which means a new species every 200 000 years or so, or co-existence of multiple species of very similar form.

Ideally, this problem should be addressed with multivariate analyses, but in most instances there is only one specimen — the type specimen — of each of the taxa in question. Our limited application of multivariate methods seems not useful. We can be certain that the sources of morphologic variation in the genus *Triceratops* were the same that we observe

today — namely individual, ontogenetic, sexual and taxonomic. On what criteria can we draw inferences about the specific sources of variation that have resulted in the morphologic spectrum encompassed in the specimens of *Triceratops*?

As a preamble to this review, it is appropriate to repeat Lull's (1913) post-facto observation:

"The practice of giving a distinct species name to every approximately complete skull, which was actually done, seems a priori unreasonable." (Our emphasis) (Lull, 1933, p. 115)

TRICERATOPS ALTICORNUS Marsh, 1887.
(= *BISON ALTICORNUS*)

This species was based on an incomplete pair of brow horn cores (U.S.N.M. 1871E) collected from the Denver formation of Colorado. First cited in 1887, it was originally assigned by Marsh to the genus *Bison*. In 1889, Marsh reassigned *alticornus* to his new genus *Ceratops* (type species *montanus*) that also was based on a pair of brow horn cores (U.S.N.M. 2411). Marsh's description of *B. alticornus* was brief and diagnostic then, but subsequent discoveries have left it inadequate today. Marsh's (1887) observations:

"This species of *Bison* is represented by various remains, the most important of which is the portion of the skull figured below. This specimen, which may be regarded as the type, indicates one of the largest of American bovines, and one differing widely from those already described. The horn cores, instead of being short and transverse, as in the existing bisons, are long and elevated, with slender, pointed ends. They have large cavities in the base, but in the upper two-thirds are nearly or quite solid. — — — The frontal region between the horn cores is broad, somewhat convex, and very rugose." (Marsh, 1887, pp. 323–324.)

Considering that no similar material had been discovered up to that time, Marsh's assignment to the well-known *Bison* was a logical choice. But with the discovery of several new specimens, Marsh soon realized his mistake. In 1889, Marsh corrected matters with the following:

"The bison-like horn cores figured in this journal probably belonged to a member of this group [Ceratopsidae], as already suggested by the writer [1889a]. They were sent to him from a locality in which he himself collected Mastodon remains and other Pliocene fossils. As they agreed in all anatomical characters with the remains of cavicorn mammals from that formation, they were referred to the genus *Bison*, under the name *B. alticornus*. The writer has since learned that they were found in the Denver beds, which, although regarded as Tertiary, are probably Cretaceous. Under these circumstances this well-marked species may be known as *Ceratops alticornus* until additional remains make certain its true nature." (Marsh, 1889b, pp. 174–175.)

Just a few months earlier, in a curious, but perhaps face-saving, statement, Marsh made the following remarks when he introduced his new species *Ceratops horridus*:

"As previously stated, the posterior pair of horn cores of this family are hollow at the base, and in form and surface markings are precisely like those of the Bovidae. The resemblance is so close that, when detached from the skull, they cannot be distinguished by any anatomical character. This accurate repetition, in later and still existing forms, of the highly specialized weapons of an extinct group of another class is a fact of much interest." (Marsh, 1889a, p. 335.)

These two statements prompted Hatcher's illuminating comments:

"The previous suggestion referred to by Marsh in the quotation just given [Marsh, 1889a] certainly does not make it clear that he at that

time considered *B. alticornus* as a member of the Ceratopsidae or as a dinosaur; and since, in his original description of the species already quoted, he clearly states that it was found in the sandstones of the Denver group it is clear that he was not misled by the collectors as to its stratigraphic position. The error was clearly one of erroneous determination of the nature of the animal to which the remains pertained, and was entirely excusable, considering the little that was then known concerning this remarkable group of dinosaurs. All that was at that time known concerning the comparative osteology of the vertebrata suggested its relations with the bisons among the Mammalia and, without making microscopical examination he would have been a daring anatomist who would have ventured to suggest from any external anatomical characters alone that these horn cores pertained to a dinosaur or other member of the Reptilia." (Hatcher, 1907, p. 116)

Although Cope (1872, '74 & '76) named the first three ceratopsians, it was with Marsh's creation of *Bison alticornus* that the bizarre group Ceratopsia came into being, despite his bovid assignment. The sequence of discoveries and designations of *Triceratops* species is central to that revelation. Hatcher (1907, p. 116) puzzled as to why Marsh did not refer *alticornus* to *Triceratops* rather than *Ceratops*, but he did not make that transfer. Perhaps he anticipated his successor, R.S. Lull, who did in their joint monograph (1907, p. 170), as he alluded on page 116: "Its affinities are certainly with the latter [*Triceratops*] genus, as will appear when we come to discuss the synonymy of the various genera." In 1933, Lull concluded that the type of *alticornus* was inadequate. In that monograph, "A Revision of the Ceratopsia", Lull accepted nine of the then-named species referred to *Triceratops* and briefly commented on three others that he termed "inadequate" because he judged them (correctly) to have been based on indeterminate material. *T. alticornus* was listed as one of the "inadequate" species. He justified that assessment:

"Here the brow horns alone must determine the specific characters, which makes a clear definition impossible. The main distinction of these horns lies in their curvature, for while anteroverged at an average slope for *Triceratops*, they are otherwise straight in lateral aspect, but slope outward and then upward in a single curve, when viewed from the front. Aside from this, there is nothing to distinguish these horns from those of several other species." (Lull, 1933, p. 128.)

These horn cores cannot be referred with any degree of certainty to any species of *Triceratops*, or indeed even to that genus or any other ceratopsian genus. The name is here considered a *Nomen dubium*.

TRICERATOPS HORRIDUS Marsh, 1889.
(= *CERATOPS HORRIDUS*)

Marsh established the species *horridus* in 1889, assigning it to his new genus *Ceratops* (1888), on the basis of an incomplete skull and fragmentary lower jaws (Y.P.M. 1820) from the Lance formation of Niobrara (formerly Converse) County, Wyoming. Marsh (1889a) noted:

"In the type specimen of the present species, the posterior horn-cores are much larger than these appendages in any other known animal, living or extinct. One of them measures at the base no less than twenty-seven inches, and about sixteen inches around, half way to the summit. Its total height was about two feet. In general form, these horn-cores resemble those of *Ceratops montanus*, but the anterior margin is more compressed, showing indications of a ridge.

The top of the skull in the region of the horn cores, is thick and massive, and strongly rugose." (Marsh, 1889a, p. 335.)

Later that same year, Marsh (1889b) established the new genus *Triceratops*, and made *horridus* the type species. (The generic distinctions registered by Marsh have been recorded elsewhere in this report under the section on the genus *Triceratops*.) In that paper, Marsh listed a number of novel features that distinguish this genus, but he did not identify those features that distinguish it from *Ceratops*. Hatcher (1907, p. 116) wondered why Marsh referred *alticornus* to *Ceratops* rather than *Triceratops*, but later (1907, p. 119) he noted the large differences in size, and also pointed out the discrepancies in stratigraphic occurrences: *C. montanus* is from near the top of the Judith River beds, 10 miles upstream from the confluence of Cow Creek with the Missouri River in north central Montana — approximately 400 miles northwest and 3500 feet lower stratigraphically from the site of *T. horridus*, which was low in the Lance formation of Niobrara County in east central Wyoming. Although they were not mentioned, those geographic and stratigraphic separations may have dissuaded Marsh from making that alignment. Hatcher repeated all of Marsh's characters of *T. horridus*, gave a thorough description of the type skull, but alluded only to the greater size, form of the brow horn cores and the shortness of the nasal horn core to distinguish *T. horridus* from *T. prorsus* and *T. brevicornus*.

Lull (1907) began his generic and specific summary of *Triceratops* by noting that he recognizes ten species under Marsh's genus *Triceratops* — including *T. alticornus* (1907, p. 168). Concerning *T. horridus*, he noted a) the rostral bone is very heavy, not so sharp as in some species along its inferior border, has a downward curved tip and has deep vascular impressions; b) the nasal horn core is very broad at the base, short and blunt compared to the most closely allied species (*T. prorsus* in which it is long and directed forward and *T. brevicornus* where it is short and stout and not very rugose); c) the supraorbital horns in *T. horridus* are very stout, long, rugose and directed forward (as in *T. prorsus*) in contrast to *T. brevicornus*.

In 1933, Lull summarized the morphology of the type skull, but did not identify any features as diagnostic. These are repeated here: muzzle fairly long, rostral very heavy with deep vascular impressions and cutting edge not so sharp and downwardly curved, nasal horn broad at the base — short and blunt with dorsal contour in line with that of nasals and anterior profile slopes slightly to the rear, brow horns exceedingly stout and rugose — probably fairly long and slope forward as in *T. prorsus*, base extremely heavy and elliptical in section, orbit seems to have been elliptical with long axis inclined at 15 degrees, jugal descending limb robust and nearly vertical with a median ridge, no trace of epijugal, jugal notch fairly deep, infratemporal opening not preserved, crest proportions not obtainable but vascular grooves on dorsal aspect, no midline prominences as in *T. serratus* as preserved. Lull concluded this section with a listing of four other specimens at other institutions that he refers to *T. horridus*: Y.P.M. 1828 (Upper Lance formation, Niobrara County, Wyoming); A.M.N.H. 5028 (Hell Creek formation, Dawson County, Montana); F.M.N.H. 12003 (Lance formation, Chalk Buttes, Montana); S.D.S.M. P271 (Short Pine Hills, Harding County, South Dakota).

As the first named and type species of the genus, it is imperative that the above "definitive" and other characters be evaluated against the "diagnostic" characters of other *Triceratops* species — and against common sense and our current understanding of species morphologic variation. These will be addressed in a summary section on the systematics of *Triceratops*.

TRICERATOPS FLABELLATUS Marsh, 1889.
(= *STERRHOLOPHUS FLABELLATUS*)

This species was established in the same paper that Marsh introduced the genus (1889b). It was based on a large skull, lower jaws and a partial skeleton (Y.P.M. 1821), also from the Lance formation of Niobrara County, Wyoming. In his description Marsh observed that this second (after *T. horridus*) specimen was of still greater dimensions and noted that:

"A striking peculiarity of this skull is the occipital crest, which extends upward and backward, like an open fan. Its margin was armed with a row of horny spikes, supported by separate ossifications, some of which were found in position.

The skull as it lay in the rock measured more than six feet in length, four feet in width, and the horn-cores about three feet in height." (Marsh, 1889b, p. 174.)

Aside from reference to the presence of epoccipitals, the only distinction from *T. horridus* is the larger size of the new form. Marsh (1889c) presented a better detailed description of the type skull in which he emphasized the "armature" (sharp cutting beak, a strong nasal horn, a pair of very large and pointed brow horns and the series of sharp projections [epoccipitals] along the rear margin of the crest). But again, the described characters are not of specific diagnostic value — at least not in our opinion.

In 1891, Marsh removed *flabellatus* from *Triceratops* and designated it the type species of a new genus *Sterrhophilus*, using the type skull (Y.P.M. 1821). Marsh's rationale is of interest:

"This restoration gives a correct idea of the general proportions of the entire skeleton in the genus *Triceratops*. The size in life would be about 25 feet in length and 10 feet in height. The genus *Ceratops* so far as is at present known is represented by individuals of smaller size, in some instances, at least, of quite different proportions. A third genus, which may be called *Sterrhophilus*, can be readily distinguished from the other two by the parietal crest, which had its entire posterior surface covered with the ligaments and muscles supporting the head. In *Ceratops* and *Triceratops* a wide margin of this surface was free and protected by a thick, horny covering." (Marsh, 1891b, p. 340.)

Hatcher (1907, p. 143) pointed out that the crest is not known in *Ceratops*. He also dismissed the second point maintaining that the immature nature of the type skull would not have allowed the development of the rugosities and other surface features present in adult skulls (implying that their absence is not necessarily evidence of a fleshy tissue covering rather than a horny covering). In his description of the skull he also pointed out that the single, undivided median foramen for the olfactory nerves (as opposed to the divided foramen in *Triceratops*) is also probably a consequence of age — the median septum in *Sterrhophilus* probably was cartilaginous in that immature specimen, and thus not preserved.

Hatcher (1907) retained the genus *Sterrholophus*, but we think it fair to conclude that he had reservations about its validity. Unfortunately, his death prevented him from completing a detailed description of the type skull and giving a final opinion. Lull completed the description:

"This species Marsh made the type of the new genus, *Sterrholophus*, because of the character of the frill, but as shown above, the peculiar absence of vascular impressions from the latter may be considered an adolescent character, which may also be said of each presumably generic feature exhibited by the skull.

The nasals are massive, but not coossified, nor was the nasal horn core ankylosed, so that this important feature is lacking." (Lull, 1907, p.171.)

It must be pointed out here that the characters that are judged to be juvenile or adolescent, and therefore invalid for generic distinction, must also be held of dubious value for specific differentiation as well. The reasoning by Lull appears to have been incomplete on this. However, Lull (1907, 1933) synonymized *Sterrholophus* with *Triceratops*, retaining *T. flabellatus* as a distinct species. It should also be noted that since the nasal horn is not preserved in this specimen, we cannot be certain that the elevated and rugose nasal pedicel on this skull really did in fact support a distinct nasal horn — which, by definition, would permit or preclude the assignment of this specimen to *Triceratops*.

Lull (1933) added further features of the type skull but refrained from labeling these of specific importance. The dorsal profile is much straighter than usual, the brow horns rise more erectly than in any other species except *T. (Diceratops) hatcheri* but their forward curvature is somewhat greater, the brow horns are laterally compressed at the base and more nearly circular in section distally, orbit is an elongate ellipse with the long axis inclined at 45 degrees, the descending limb of the jugal is broad and without a keel, jugal notch is not deep, infratemporal fenestra is a broad oval, the face is deep and of moderate length, muzzle is very short, rostral and predentary are both missing, the crest while wide for its length appears narrow due to the crest curvature, there is no trace of vascular impressions except behind the supratemporal fenestrae, there are 19 epoccipitals, maxillary teeth appear to number 35, dentary teeth 30, the mandible appears slender for the skull, the coronoid process is expanded at its summit.

The type skull appears to be the only one, for Lull did not list any others referable to this species. At this writing, we know of no other material referable to *T. flabellatus*, but we have not made an exhaustive search.

TRICERATOPS GALEUS Marsh, 1889.

Announced by Marsh in the same paper that he proposed *T. horridus* and *T. flabellatus*, this species is unquestionably the least well-founded of all the species referred to *Triceratops*. It is based on a small nasal horn core (U.S.N.M. 2410), probably from the Denver formation near Brighton, Colorado. Marsh's (1889b) description is not diagnostic:

"In this species, the nasal horn-core is especially characteristic. It is compressed longitudinally, and its apex is pointed, and directed well forward. It is on the extremity of the nasals, and is thoroughly coossified with them. In front, at the base, it shows indications of union with

the premaxillaries, but this connection was slight." (Marsh, 1889b, p. 174.)

Hatcher (1907, p. 132) noted that the extremely fragmentary nature of the material upon which this species was founded precludes any possibility of definition. He concluded "The species should be abandoned." Without comment, Lull (1907, p. 168) concurred with Hatcher.

In his 1933 monograph, Lull did not even list *T. galeus* among his "inadequate" species. Only in his introductory remarks to the "inadequate" species did he mention *T. galeus* as based on a single nasal horn core and that Hatcher had already discarded it as based on insufficient evidence. There is no question that this fragment cannot be referred to any ceratopsian species with any degree of certainty. Therefore, *T. galeus* is here designated a *Nomen dubium*.

TRICERATOPS SERRATUS Marsh, 1890.

The fifth species of *Triceratops* to be designated was *T. serratus*, based on a large and complete, well-preserved skull and jaws (Y.P.M. 1823) from the Lance formation of Niobrara County, Wyoming. The type skull measures 1.8 m in length although apparently not fully adult. Marsh noted the following specific characters:

"A striking peculiarity of this skull, which has suggested the specific name, is a series of bony projections on the median line of the parietal crest. The latter is elevated along this line to support them, and the sides descend rapidly to their union with the squamosals. There is a second series of elevations along the middle of the squamosal bone as it falls away from the base of the horn-core, but these are much less prominent.

The orbit is nearly circular, instead of oval, and is situated above and forward of its position in the species referred to. The quadrate-jugal meets the anterior process of the squamosal, forming a closer union than in the skull previously figured. In this respect and in the elevations on the squamosal it approaches a much smaller specimen, at present referred to the genus *Ceratops*.

The nasal horn-core is wanting in the present specimen, as it was not ossified with the nasals. It projected upward and forward. The nasal bones extend outside the superior branch of the premaxillaries, the lateral suture uniting the two being nearly vertical." (Marsh, 1890a, pp. 81–82)

The absence of the nasal horn core presents exactly the same problem raised in the case of the type skull of *T. flabellatus*. Can we be certain that there ever was a nasal horn core in the type skull?

Following a detailed description of the type skull, Hatcher (1907, p. 126) concluded:

"The characters which at present seem most distinctive of this species are (1) the position of the lachrymal foramen which lies between the maxillary and nasal instead of within the maxillary; (2) the structure of the inferior temporal arch; (3) the comparatively slender supraorbital horn cores; (4) the narrow and elongated lateral temporal foramen. The number of epoccipitals and the rugosities mentioned by Marsh as present on the squamosals may also prove to be of specific importance." (Hatcher, 1907, p. 126)²

2) On the same page, immediately before the above quoted summary, Hatcher observed: "The number of epoccipitals may, however, have varied in different individuals and can hardly be considered as diagnostic of the different genera or species." (Hatcher, 1907, p. 126)

In his review of the taxonomy of the Ceratopsia, Lull (1907) added the following characters to *T. serratus*:

"The rostral bone is rather small, lighter and less rugose than in the other species; this, however, may be either a juvenile or possibly a sexual character. The nasal horn core is wanting in the type, having been lost at the suture between it and the nasals. It must, however, have been considerably compressed transversely. The supraorbital horn cores are slender and much more erect than in most species, somewhat elliptical in section at the base and more nearly circular in their mid-length. The orbit is large and irregularly elliptical in outline, its long axis running obliquely downward and forward. The position of the orbit is in advance of and superior to that of *T. (Sterrhophilus) flabellatus*. The lachrymal foramen lies between the nasal and maxillary, as in the last mentioned species." (Lull, 1907, p. 169)

Lull (1933) observed the following additional conditions in the type skull: muzzle and face long, profile of face and crest in line with each other, orbit a broad ellipse inclined 45 degrees, descending limb of jugal narrow then expands slightly near extremity without a keel and nearly vertical, jugal notch deep, infratemporal fenestra large and nearly quadrangular, preorbital fenestra (= lachrymal foramen) between nasal and maxillary, rostral small lighter and less rugose than in other forms with inferior border nearly horizontal rather than curved downward, rostral deeply excavated ventrally and with fairly sharp but irregular cutting edge, nasal horn a separate ossification and lost, brow horns slender and more erect than in any others except *T. flabellatus*, a boss-like prominence at the base of the horn which is first of a series in an oblique line to the proximal third of the squamosal, horn base elliptical and nearly circular distally, crest seems wide in proportion to length due to transverse curvature of the crest, seventeen epoccipitals, maxillary and dentary teeth number about 28, mandible slender, coronoid process moderately expanded distally.

Lull lists no additional skulls referred to this species.

TRICERATOPS PRORSUS Marsh, 1890.

In the same paper that he described *T. serratus*, Marsh proposed still another species of *Triceratops* on yet another complete skull and jaws (Y.P.M. 1822), but this specimen was associated with six cervical vertebrae. The specimen was collected from the Lance formation also from Niobrara county, Wyoming. Marsh described it as follows:

"The nasal horn-core and the rostral bone are in position, and perfect. The former is very large, and is directed straight forward, its upper surface being nearly on a line with the superior face of the nasals. It is somewhat oval in transverse section, and pointed in front, the apex being directly above the anterior extremity of the rostral bone. It is so firmly coössified with the nasals that no trace of a suture can be observed. Its external surface is rugose from vascular impressions, indicating that it was covered by horn, thus forming a most powerful weapon.

The huge frontal horn-cores are more massive, and less slender, than in the species above described.

The parietal crest is not so broad as in the two species last described, but appears to resemble more strongly that of *Triceratops horridus*, its sides being inclined downward, as if to protect the neck.

The rostral bone, likewise, is very similar to that in the last species, but is somewhat more compressed. The two forms may be readily distinguished by the nasal horn-core, for in *T. horridus*, this is compara-

tively small, and points directly upward, instead of straight forward, as in the present species." (Marsh, 1890a, p. 82)

Because of the Munich specimen reported on elsewhere here, it is worthwhile to include the rest of Marsh's description of *T. prorsus* even though it adds nothing of value in distinguishing between the various species of *Triceratops*, because this is one of the few type specimens that includes postcranial material.

"With this skull were found several cervical vertebrae, and some other portions of the skeleton. The atlas, axis, and third vertebra are firmly ankylosed with each other, and their ribs also are coössified in the same mass. This union, unknown hitherto among the Dinosauria, was evidently rendered necessary to afford a firm support for the enormous skull. The remaining cervical vertebrae are short and massive, and the articular faces of the centra are concave or nearly flat." (Marsh, 1890a, p. 82)

Brief though this description is, it applies equally well to *T. brevicornis* as well as *T. prorsus* and most other ceratopsids. Hatcher (1907) gave a detailed description of the type skull which he summarized as follows:

"The present species, which includes nearly the smallest if not the very smallest representative of the family known from the Laramie [= Lance] formation, is readily distinguished by the following characters: (1) The long and anteriorly directed nasal horn core; (2) the slender supraorbital horn cores directed upward, forward, and outward throughout about one-half their length, when they begin and continue to curve gently inward from thence to the summit; (3) the nearly circular orbit; (4) the position of the infraorbital foramen [= lachrymal foramen] below the superior border of the ascending branch of the maxillary, as in *Sterrhophilus flabellatus*." (Hatcher, 1907, pp. 128-129)

Lull (1907) repeated these and added some additional features:

"The rostral bone is contrasted with that of *T. horridus* in being somewhat less massive and having a sharp cutting edge, as contrasted with the blunt margin in the other. The inferior margin curves downward toward the point, in agreement with *T. horridus* and *T. brevicornis*. — — —

The lachrymal foramen is entirely within the maxillary bone, as in *T. (Sterrhophilus) flabellatus*, in contrast to its position between the maxillary and nasal as in *T. serratus*, *T. brevicornis* being in a sense transitional between the two types, while the condition which obtained in *T. horridus* can not be determined, as this part of the specimen is lacking.

The frill is deeply arched transversely, ranging through an arc of 27 degrees, with seven lateral and one median epoccipitals, making fifteen in all. The quadratojugal notch is deeper than in any other known species, and the postfrontal (pineal) fontanelle is entirely closed. Posteriorly the frill border was free, for vascular impressions occur on its inferior face for a distance inward of 20 cm from the margin. This feature, together with the closure of the postfrontal fontanelle, may be characteristic of old age, but in some old skulls of other species the fontanelle seems to be persistently open." (Lull, 1907, p. 169)

In his 1933 monograph Lull noted that the type skull was that of an aged individual, yet it was the smallest *Triceratops* specimen known. He further described it as follows:

"The orbit is nearly circular — — — but the slightly longer axis slopes as usual at an angle of about 45 degrees from the perpendicular. The descending limb of the jugal is narrow and tapering, without a median keel, and the axis is inclined slightly backward. The jugal notch is fairly deep and wide, the infratemporal opening being of average size and somewhat triangular, with curved margins. The rostral is large — — — with a sharp cutting edge and downwardly curved inferior margin. The muzzle is rather short, although the face is long. The most distinctive feature of *prorsus* is the nasal horn, which is long and directed forward so that its tip extends over the forward margin of the rostral — — —. This nasal horn is unique — — —.

The brow horns are slender, directed upward, outward and forward for half their length, and then curved gently inward and upward toward their tip — — —.

The crest is deeply arched, and helmet-shaped, with an undulating dorsal line which is concave upward. — — — A characteristic feature which links *prorsus* and *brevicornis* is the limitation of the vascular impressions on the inferior surface of the crest to a very clearly defined marginal zone averaging 15–17 cm in width.

The preorbital fossa [= lachrymal foramen] lies entirely within the maxillary; the ascending process of the premaxillary, although long and slender, does not quite reach it. The pseudopineal fontanelle is utterly lacking — — —. This, apparently is not a matter of age, for the *flabellatus* specimen is extremely young, and no matter what the age of other skulls, young or old, it is always present. The mandible is rather slender, with a high coronoid process, expanded fore and aft at the summit. The number of vertical rows of teeth is, in the maxillary about 30, in the mandible, about 33." (Lull, 1933, pp. 117–118)

Of particular importance is Lull's final comment on *T. prorsus*, in which he notes that it is a very popular name, and is used repeatedly in identifying material. He observes that despite that popularity, there is only one skull — the type skull — that is referable without question to this species. More will be said about this later.

TRICERATOPS SULCATUS Marsh, 1890.

A seventh species of *Triceratops* was erected by Marsh on a poorly preserved skull, jaws, several vertebrae and some limb material (U.S.N.M. 4276) from the Lance formation of Niobrara County, Wyoming. Marsh judged this to be a fully adult specimen because of the ossification of the epoccipital and epijugal bones to the skull. The distinguishing features of this species listed by Marsh were:

"The most distinctive character of the skull is seen in the horn-cores of the frontal region, which are very large and elongate. On the posterior surface of the upper half of each horn-core, there is a deep groove, which has suggested the specific name. The horn-cores are narrow in front, and in the upper portion become distinctly ridged. The antero-posterior diameter of the horn-cores at the base is about nine inches, and above, where the groove begins, about four and a half inches.

The caudal vertebrae in this species are unusually short, and the median caudals have a deep longitudinal groove on the bottom of the centra." (Marsh, 1890b, p. 422)

Hatcher (1907) noted that the only supraorbital horn core of the type skull that is presently available does not agree very well with Marsh's description of a deep groove on the posterior surface of the upper half of each horn core. Hatcher concluded that Marsh based his description on the missing horn core (despite the fact that Marsh stated "each horn core"). He further noted that the existing horn core appears to have been injured, broken off during life. Referring to two other partial skulls in the U.S.N.M. collections that have been referred to *T. sulcatus* (U.S.N.M. 4286 and 1203, 1206–1210) which show prominent longitudinal grooves in the upper parts of the supraorbital horn cores, he noted that these varied. In one case, the grooves are on the anterior-interior surface (rather than the posterior surface as described by Marsh in *T. sulcatus*). In the other example, similar grooves occur on both the anterior and posterior surfaces. Hatcher's conclusion:

"In view of the fact that as shown above, grooves similar to those described by Marsh as characteristic of the present species may occur at various places on the supraorbital horn cores of the Ceratopsidae,

it does not seem advisable to consider either the presence or the position of such grooves as of specific importance. It is probable that such grooves have, in most instances at least, had their origin in an infolding or thickening of the horny sheath with which in life the horn core was encased, and their position, form, and depth were determined by the place, nature, and amount of thickening or infolding of the horny substance. Such being their origin, as appears not improbable, they are likely to appear in any of the various genera and species, and should not be considered as of specific importance." (Hatcher, 1907, p. 134)

Lull (1907) summarized the situation with regard to the type skull and registered Hatcher's opinion. He concluded:

"On the whole there seem to be no characters in the fragmentary material representing the type which afford a basis for a true specific diagnosis. It would be well, therefore, to await the discovery of additional material before deciding as to the validity of this species." (Lull, 1907, p. 170)

It hardly seems necessary to wait for further discoveries because the diagnostic feature (posterior grooves in the brow horn cores) have been shown to be inconsistent in the type specimen and of variable occurrence in other specimens. Validation of such grooves in future finds cannot be demonstrated as identical to those of the type (one of which is lost). In 1933, Lull repeated the variable occurrence of horn sulci in several ceratopsian specimens and concluded as before:

"At present, therefore, the species *Triceratops sulcatus* cannot be defined." (Lull, 1933, p. 129)

Other than the fragmentary specimens cited above, Lull mentioned no other specimens referable to *T. sulcatus*.

We conclude that *Triceratops sulcatus* is a *Nomen dubium*.

TRICERATOPS ELATUS Marsh, 1891.

Marsh's original description of this species is based on a single skull (U.S.N.M. 1201) from the Lance formation of Niobrara County, Wyoming. Less than definitive, that description reads as follows:

"Although this skull is about 6½ feet in length, it belonged to an animal scarcely adult, as indicated by some of the cranial sutures. The rostral bone is not coossified with the premaxillaries as in old animals, and the superior branch of the former bone has its extremity free. The nasal horn-core, however, is firmly coossified with the nasals. It is of moderate size, with an obtuse summit directed upward. The main horn-cores were quite long, with their extremities pointed and directed well forward. These horn-cores are compressed transversely, the section being oval in outline. One of the most striking features of the skull is the parietal crest, which was quite elongate and much elevated, more so than in any of the species hitherto discovered, and this has suggested the specific name.

The length of this skull from the front of the rostral bone to the back of the parietal crest was about 78 inches, and the greatest transverse expanse of the posterior crest was about 40 inches. The summit of one of the frontal horn-cores was about 28 inches above the orbit and 53 inches from the base of the quadrate." (Marsh, 1891 a, p. 265.)

To these Hatcher (1907) added the following:

"The most striking specific characters are to be seen in the nasal and supraorbital horn cores and the jugal. — — — The orbit also is exceptionally large, having a vertical diameter of 175 mm and an antero-posterior diameter of 150 mm. The infratemporal fossa is much elongated antero-posteriorly and is triangular in outline. Its greatest antero-posterior diameter measures 145 mm and its greatest vertical diameter has a length of 85 mm.

Epoccipitals were borne only on the posterior margins of the parietals and the posterior half of the squamosals. — — Each squamosal supported four epoccipitals, and there were six on the parietals, three on either side of the median line. Apparently there was no median epoccipital as in *T. prorsus* and other species. The nasal horn core is very short and stout, rising but little above the superior surface of the nasals — — — the nasal horn core is seen to have originated from a center of ossification distinct both from the nasals and the premaxillaries. In a second specimen belonging to a younger individual, which I shall consider as a cotype, U.S.N.M. 4805, found on the same horizon and only a few feet from the type, the nasal horn core is disarticulated and the sutural surfaces at the base for contact with the premaxillaries and nasals are very distinct.

The jugal is especially characteristic in the present species. The inferior process, instead of descending vertically beneath the orbit, as in most other species of the *Ceratopsia*, is directed downward and backward at an angle of about 45 degrees, and the distal end is produced far back of the posterior border of the orbit. The posterior border of the inferior process of the jugal is regularly but gently convex, the anterior concave." (Hatcher, 1907, pp. 135–136.)

Lull (1907) simply repeated most of the features noted before by Marsh and Hatcher. But in 1933, he elaborated on the earlier descriptions:

"The muzzle is rather slender and of moderate length although the rostral is fairly large. The latter has deep vascular grooves and a comparatively straight inferior margin which points decidedly downward toward the tip. The narial opening is very large. The nasal horn is peculiar, although resembling that of *calicornis* — — — The horn core, while bearing vascular impressions, is truncated, the anterior and superior margins being at right angle with each other. — — —

The brow horns are long and massive, extremely heavy at the base where they are strongly compressed laterally, becoming more circular toward the tip. The rear of the base bears a marked prominence, as in *calicornis*, *obtusus* and *serratus*. The horn curves strongly forward, reversing slightly toward the extreme tip.

The orbit is a broad oval of regular outline, with the broader end uppermost and inclines at an angle of about 15 degrees out of the perpendicular. The jugal is unique in that it is J-shaped, having no posterior limb, as in every other ceratopsian skull — — — The descending limb is long and rather narrow, with curved, nearly parallel front and rear margins. The longitudinal ridge, which is but slightly developed, lies near the rear instead of being in the center of the bone. The jugal notch is deep and wide, and the infratemporal fossa unusually large and triangular, with the apex pointing toward the orbit." (Lull, 1933, p. 122.)

Lull concluded this discussion by noting that another skull (U.S.N.M. 2100) may be referred to this species, as well as a possible second specimen (A.M.N.H. 5116) now displayed in a composite mounted skeleton. Lull's final statement on this species is especially worthy of repeating here:

"There is infinite variation in all *Triceratops* skulls." (Lull, 1933, p. 123.)

TRICERATOPS CALICORNIS Marsh, 1898.

This species was based on most of a skull, jaw and parts of a skeleton (U.S.N.M. 4928) from the Lance formation, again from Niobrara County, Wyoming. Marsh's description reads in part:

"The skull as a whole shows the well-marked features of the genus *Triceratops*. A specific character is seen in the nasal horn-core, which is in perfect preservation. It is directed well forward, and unlike any hitherto described is concave above, which fact has suggested the spe-

cific name. The upper or posterior surface of this horn-core somewhat resembles the bottom of a horses hoof.

Some of the principal dimensions of this skull are as follows: length from front of beak to back of parietal crest, about six feet, five inches; from front of beak to end of occipital condyle, three feet, five inches; distance from occipital condyle to back of parietal crest, four feet; from front of beak to point of nasal horn-core, twenty-three inches; height of post-frontal horn-core, twenty-nine and a half inches, and antero-posterior diameter of same horn-core at base, twelve inches." (Marsh, 1898, p. 92.)

Hatcher (1907) noted that most of the characters seen in the type skull of *T. elatus* which might be considered of specific importance are also present in the type of this species, though perhaps somewhat more emphasized, as in the case of the nasal horn which led Marsh to the specific name. Lull (1907) also drew a comparison of *T. elatus* with *T. calicornis*, but did not note different skull proportions with much longer premaxillaries and a larger rostral bone in *T. calicornis*. He also noted that the descending process of the jugal is more nearly vertical, as in other species, rather than inclined backward. However, Lull did add Hatcher's explanation that this might have been due to preservation (pressure) differences in the two.

In his "*A Revision of the Ceratopsia*" (1933), Lull observed that the type specimen was one of the largest *Triceratops* skulls on record with an overall length of six feet 10 3/4 inches and yet in his view was not fully adult. Attention was drawn to the disproportionately long muzzle. Lull also recorded:

"The orbit is an elongated ellipse — — — inclined at an angle of about 15 degrees. The jugal is of medium width, and tapers to a point in the distal half. It differs from that of *elatus* in having the usual rear branch above and is therefore T-shaped — — — There is a slight longitudinal ridge — — — The jugal notch is of moderate depth, but is wide with a curved outline.

The infratemporal fossa [= fenestra] is rather small for the size of the skull and differs, not only in this, but also in shape, from that of *elatus*, being oval in form, with a rather long apex pointing downward and forward. — — — The narial opening in *calicornis* is very large in correspondence with the large muzzle. The rostral is also large, with a very convex profile. The downwardly curving inferior margin is rather sharp-edged. — — — The brow horns are large, agreeing with those of *elatus* in size, massiveness, and general curvature, and in the possession of a boss-like prominence on the rear of the base. They have a very heavy base from which they taper rapidly, curving sharply forward but without the reversed curve toward their tip. The crest is only partially preserved — — — There were probably the usual number of epoccipitals, perhaps 19 in all, although but two are preserved. A few shallow vascular impressions are present on the upper surface of the crest. Below they are deeper, especially in the posterior part of the squamosal, and extend further in from the margin, there being no limited zone of vascular grooves — — — The crest is unusually wide when viewed from above, being over twice as wide as long, according to Hatcher's figure. The pseudopineal fontanelle is present and large. — — — The preorbital fossa [= lachrymal foramen] lies between the nasal and maxillary, and is reduced to a rather wide, elongate slit.

The dentaries are of great size — — — There are 38 rows of teeth in the left dentary, opposed to 28–32 in the maxillary, the exact number being difficult to determine. — — —" (Lull, 1933, p. 124.)

Lull did not mention any other skulls that he considered to be referable to *T. calicornis*, but the authors are aware that the Field Museum, Chicago, has a skull (F.M.N.H. P12003) lacking the lower jaws, that has been identified as belonging to this species.

TRICERATOPS OBTUSUS Marsh, 1898.

The final species of *Triceratops* to be designated by Marsh is represented by a large skull and jaw fragments (U.S.N.M. 4720), also from the Lance formation of Niobrara County, Wyoming. As reported by Hatcher (1907), the type material consisted of a pair of dentaries, the anterior portion of the nasals, a left maxillary, a squamosal, parts of a pterygoid and a single vertebra. Marsh's necessarily terse description emphasized the nasal horn and is as follows:

"The nasal horn-core of this skull is very short and obtuse, and is so well preserved that it indicates the normal form and size. The entire length of this horn-core is only one inch. Its summit is three and a half inches behind the premaxillary suture. The width of the nasals beneath the horn-core is five and a half inches. The length of the squamosal from the quadrate groove to the posterior end is about thirty-six inches and its greatest width is nineteen inches." (Marsh, 1898, p. 92.)

This was followed by Hatcher's (1907) somewhat more comprehensive description:

"The specific name was suggested by the character of the nasal horn core. The nasals, as shown in the accompanying figures, are extremely broad, and the nasal horn core is reduced to a broad, rounded, and rugose prominence, marked with a number of deep vascular grooves.

The dentary is exceptionally deep and the teeth are unusually large. Below the base of the coronoid process on either dentary the external surface of the bone presents a very sharp ridge that extends continuously throughout about one third of its length. — — — The mandibular fossa extends rather farther forward than is common in other species of the Ceratopsia. The dentary is exceptionally massive and the teeth are very large. There are a number of foramina on the external surface of the dentary, as shown in the accompanying figure.

Notwithstanding the scanty and fragmentary material upon which the present species is based, it would seem to be a valid one, as indicated alike by the characters of the dentary, the teeth, the nasal horn core, and that part of the nasals still preserved." (Hatcher, 1907, p. 140.)

The two descriptions by Marsh and Hatcher of such fragmentary material left much to be desired — especially since they were discussing the basis of a distinct species. Of course we may forgive them because they were dealing with some of the first specimens of a poorly represented and understood group. What is surprising and more disturbing is that neither author mentioned that there was much more to the type specimen than Hatcher reported. Gilmore (1919) noted that the type consists of "nearly the entire skull" and even though it was collected by Hatcher that fact "obviously escaped his memory, as no allusion is made to it in any of his writings". Gilmore reports:

"The finding of nearly the entire remaining parts of the skull (see pl. 4) is a welcome addition to the above material, and it now places the type on an adequate foundation for comparison with the other and better known species.

Although somewhat distorted laterally [sic] by pressure the skull is essentially complete, lacking only the rostral, premaxillary bones, and the median portion of the frill or demossupraoccipital [sic].

That the skull belongs to the same individual as the type is shown by the similarity of the labels accompanying both, by the unusual bright yellowish color of the bones and also by the finding of fragments of the skull that fitted the dentaries, and fragments with the nasals and dentaries that were fitted to the skull." (Gilmore, 1919, pp. 98–99.)

Needless to say, it is fortunate that Gilmore was able to recognize and re-associate the separated parts of the type skull

of *T. obtusus*. He also relocated the missing squamosal that Hatcher could not find. In all probability, these several separations resulted during the transfer of several *Triceratops* specimens (and other fossil material) from Yale to the National Museum at the Smithsonian after Marsh's death in 1899. Whatever the cause, we are still faced with the fact that a distinct species was founded on insufficient evidence. After comparing the re-united skull with other better known species, Gilmore observed:

"The characters pointed out by Hatcher for distinguishing this species are for the most part of a trivial nature and little dependence can be placed on them as representing constant specific differences. — — — Of the specific characters pointed out by Hatcher, the reduced nasal horn core alone is probably valid, though it may be only a sex character. — — — After a careful comparison of this additional material of *T. obtusus* with the several types in the United States National Museum collections, and with the figures and descriptions of the other species of the genus preserved elsewhere, I am unable to detect characters that would satisfactorily distinguish this species." (Gilmore, 1919 p. 100.)

To turn back for a moment, Lull (1907) apparently agreed with Hatcher, noting the distinctive nature of the nasal horn core and the exceptionally deep and massive dentary and the teeth of unusually large size. But it is important to note Lull's remarks in 1933 concerning the nasal horn in *T. obtusus*.

"The nearest ally of *Triceratops obtusus* seems to be *horridus*, the main distinction between them lying in the nasal horn which varies considerably among the several skulls attributed to the latter species [our emphasis], although never to the point of obsolescence. In its loss of nasal horn and great size, *obtusius* is specialized; otherwise it is a generalized type. It is interesting to see the reduction of the nasal horn so low in the Lance series, as this debars *obtusius* from the ancestral line of any other species except perhaps *T. (Diceratops) hatcheri*, which occurs two-thirds of the way up from the bottom of the sequence. That it constitutes a valid species is shown by a detached nasal horn of quite similar character in the Peabody Museum collection, No. 1825. This horn is straighter on top and with a less rounded apex when viewed laterally. It cannot be attributed to any other species than this." (Lull, 1933, pp. 125–126.)

As we emphasized in this quotation, Lull notes the great variation in the nasal horn in what he terms as the nearest allied specimens (which he identifies as *T. horridus*), and yet he still seems to claim that the nasal horn is sufficient criteria for distinguishing between species. That conclusion, in our opinion, is not reinforced by his claim that an isolated nasal horn in the Yale collection is referable only to *T. obtusus* and therefore validates this species. Notice that elsewhere in this same monograph he acknowledged the invalidation of another species of *Triceratops* (*T. galens*) because it was based on an unassignable isolated nasal horn core!

Elsewhere in his discussion of *T. obtusus*, Lull (1933) provides these details:

"The type is an old individual with an estimated length of at least 7 feet, hence one of the largest on record. The muzzle anterior to the nasal horn, however is missing, and the length of this region is subject to considerable specific variation. — — — The orbit is large, a rather elongated ellipse, the axis of which is inclined at an angle of about 30 degrees from the perpendicular.

The descending limb of the jugal is very broad for its length, and has a marked median ridge. The jugal notch is rather shallow and wide, and the infratemporal fossa [= fenestra] very small for the size of the skull, triangular in shape, with the apex toward the rear. The nasals are very broad, especially over the posterior limit of the nares, and the two sides converge rapidly toward the anterior end. The nasal horn is reduced to a rather broad, rounded rugose prominence, with deep

vascular grooves. Laterally, the nasal profile reminds one of that of *Arrhinoceratops* of the Edmonton formation. — — —

The brow horns are very massive at their base, and have a protuberance at the rear as in *elatus* and *calicornis*. But they are relatively shorter, and lack the great forward curvature of the horns of these species. The horns of *obtusius* also resemble somewhat those of *brevicornus*, but they are relatively less stocky and taper to a longer point without showing a reverse curve.

The crest is only partly preserved — — —. There are deep vascular grooves on the dorsal surface of the crest and on the under surface of the squamosal. They are not limited beneath to a peripheral zone. Epoccipitals must have been present, although now the margin of the squamosals is smooth, without undulations. The mandible is very robust with a low broad coronoid. The number of mandibular tooth rows is 28, that of the maxillary — — — cannot be determined. Individual teeth are very large." (Lull, 1933, p. 125.)

From the preceding, it should be apparent that *T. obtusius* is a very doubtful taxon. First, it was established on only a small fraction of the available material because of the peculiarly abbreviated nasal horn core. At this point it must be pointed out that rather than a horn core this protuberance appears to be just a boss or swelling on the nasals, and is qualitatively like that of *T. (Dicreratops) hatcheri*. The isolated nasal horn in the Yale collections mentioned by Lull has no relevance, and as we quoted Lull, he himself noted the considerable variation in the nasal horn in these specimens. Second, the deep form of the dentaries and the unusually large teeth are both growth dependent. Note that this type specimen is one of the largest skulls on record. We agree with Gilmore that the specific characters cited by Marsh and Hatcher are of a trivial nature and not likely to have taxonomic significance.

TRICERATOPS BREVICORNUS Hatcher, 1905.

It is historically noteworthy that this is the first species of *Triceratops* not to be named by Marsh. Further, it is appropriate that this particular species (the type specimen of which is the primary subject of this study) was the only one to be named by Hatcher — the man responsible for the discovery and collection of nearly all of the type specimens of the named species of *Triceratops* reviewed here. More than any other individual, John Bell Hatcher must be acknowledged as the discoverer of horned dinosaurs.

The present species is based on a nearly complete skull with lower jaws, a nearly complete presacral series of vertebrae, rib fragments and fragments of a pubis (B.S.P. 1964 I 458; formerly Y.P.M. 1834). It was collected by Hatcher from near the top of the Lance formation of Niobrara County, Wyoming. Hatcher listed the following as distinctive characters:

"Supraorbital horn-cores short and stout, not much compressed, nearly circular in cross section. Nasal horn-core short and stout with the anterior border perpendicular instead of being directed upward and forward at an angle of 30 degrees. Vertical and longitudinal diameters of lateral temporal foramen nearly equal. Orbit irregularly elliptical in outline with the longer axis running from above downward and forward. Post frontal fontanelle open, even in old individuals." (Hatcher, 1905, p. 413.)

Hatcher (1907) noted that the extremely rugose nature of the skull, together with the obliterated closed condition of the cranial sutures certify that this specimen was that of an old individual. As in *T. serratus*, the lachrymal foramen lies bet-

ween the nasal and maxilla, but the latter encloses the anterior half and forms half of the upper border of the foramen. The rostral bone is heavy and deeply excavated beneath. The lateral temporal fenestra is not unusual, and triangular in outline. Hatcher (1907) failed to designate specific features beyond those cited in his original announcement.

Lull (1907) added the heavy nature and ventrally excavated form of the rostral, the condition of the lachrymal foramen, and noted that the frill is elevated rather sharply toward the posterior margin and bears nineteen epoccipitals, six pairs on the squamosals (as compared to fifteen in *T. prorsus*) — which may or may not have taxonomic significance.

In 1933, Lull added considerably to the description of this species, but again, most of the features noted were not explicitly designated of specific distinction. It is more a description of one skull (which had been designated the type) than a diagnosis of *T. brevicornus*. It reads as follows:

"The skull proportions resemble those of *prorsus*, except that the muzzle is relatively longer in proportion to the face. The dorsal profile of the entire skull forms a more or less continuous line, the crest rising in a gentle curve toward the rear. The rostral is proportionately very heavy, with a deeply excavated inferior surface; the cutting edge is rather sharp, but comparatively straight, although pointed downward toward the tip. The descending limb of the jugal is narrow and parallel-sided, while the rather blunt median keel divides the jugal into equal halves. The jugal slopes gently backward. The jugal notch is deep and wide, and the infratemporal opening is large and triangular, with the rounded apex behind. The orbit is an elongated ellipse, with the long axis forming an angle of about 15 degrees with the perpendicular. The nasal horn is short and very stout, rather prominent but smaller than in *prorsus*, and it does not extend forward over the rostrum as in the latter species. The long diameter is much greater than the transverse. The dorsal profile of the horn core is continuous with that of the nasal bones and sweeps upward in a gentle curve into that of the horn. The anterior margin is somewhat convex and is inclined forward toward the tip of the horn.

The brow horns are short, stout and abruptly tapering, more nearly circular at the base than in any other species except the specimen of *elatus*, No. 2100 U.S.N.M. Contrasted with the longer horns of *prorsus* and *horridus*, they curve gently forward and outward.

The crest of *brevicornus* is not very long, being proportionately shorter than in *prorsus*, and not so sharply curved transversely as in the latter species. — — — The number of epoccipitals is 19 for *prorsus*, and 17 for *brevicornus* [he counted 19 in 1907]. The number of maxillary teeth also correspond at 30. The mandible is of medium proportions, the coronoid process is rather low and not much expanded at the summit, in contrast to that of *prorsus* which is high with a marked expansion. The prementary is heavy to match the jaw, and rather sharply pointed.

The preorbital fossa [= lachrymal foramen] seems to lie entirely within the maxillary, although the ill-defined sutures make this difficult to determine with certainty." (Lull, 1933, p. 119)

Lull registered a single additional skull now in the Carnegie Museum (C.M.N.H. 1219) as the only other one known to him that is undoubtedly referable to *T. brevicornus*.

Hatcher (1905) did not mention another less well preserved fragmentary skull (Hatcher's skull nr. 21) in the Yale collections (Y.P.M. 1832) which bears a label "plesiotype". It is clearly referable to *Triceratops* and is comparable in size to B.S.P. 1964 I 458, but provides no significant additional information. It is curious that neither Hatcher (1905) or Lull (1933) mention this specimen at all, even though it apparently was considered worthy of special designation as the "plesiotype".

TRICERATOPS HATCHERI Lull, 1907.
(= *DICERATOPS HATCHERI*)

The type specimen, a skull without the lower jaws (U.S.N.M. 2412) was collected by Hatcher from the Lance formation of Niobrara County, Wyoming. The specimen was first described by Hatcher (1905), but he failed to provide a name. Lull (1907) repeated Hatcher's description and designated it the type of a new genus and species, *Diceratops hatcheri* (see also Lull, 1905). In his original description, Hatcher gave the following specific characters:

"Supraorbital horn cores short, robust, and nearly circular in cross section at the base, erect and but slightly curved. Orbits project in front of the horns, the frontal region lying between the horns being concave. Exoccipital processes slender and widely expanded." (Hatcher, 1905, p. 417.)

The generic characters noted by Hatcher consisted of:

"Nasal horn core absent. Squamosal bones pierced by large fenestrae, while smaller ones penetrate the parietals. The inferior border of the squamosal lacks a quadrate notch." (Hatcher, 1905, p. 417.)

In describing the type skull in 1907, Hatcher noted in addition the small size of the rostral and its coossification with the premaxillaries, the maxillaries are massive, the lachrymal foramen is below and well forward of the orbit, the supratemporal fenestra is elongate and the lateral fenestra has equal vertical and longitudinal dimensions.

Lull (1907) noted that by the absence of a nasal horn core *Diceratops hatcheri* resembles *T. obtusus*, "though evidently not synonymous therewith". Why not? Lull made some interesting but inconclusive statements concerning this specimen:

"The fenestrated parietals would seem to point to primitive conditions until one notes the presence of similar fenestrae in the squamosals, a character which here appears for the first time. This, together with the fact that the squamosal fenestrae are of unequal size — which may also have been true of those of the parietals, as only the right is preserved³⁾ — leads one to conjecture whether they may not have been secondarily acquired and together with the vestigial nasal horn, may not be evidences of high specialization from some *Triceratops* like ancestor." (Lull, 1907, p. 163.)

In an appended footnote to this quotation, Lull informs the reader that he "is now firmly convinced" that all these apertures through the frill of *Diceratops* are pathologic, having been caused either by wounds or disease, citing similar perforations in the right frontal of the type of *T. serratus* and in the squamosal of the type of *T. elatus*. Lull then lists the features by which he distinguishes *Diceratops* from its nearest ally, *Triceratops*:

" — — — by the much smaller rostral bone; by the absence of the nasal horn, which in all species of *Triceratops* except *T. obtusus* is fairly well developed; by the very erect, short, robust supraorbital horn cores, which seem to take their origin much further back with relation to the orbit; by the concavity of the frontal region between the orbits; and finally, by the peculiar form of the persistent postfrontal (pineal) fontanelle suggestive of that of the genus *Torosaurus*. — — — Another distinctive feature is in the very erect position of the descending process of the jugal, which is directed slightly forward instead of downward and backward as in *Triceratops*." (Lull, 1907, p. 163.)

3) A misleading intrusion here since the suggestion cannot be verified or refuted.

In 1933, Lull repeated these differences and added further details as follows:

"The inferior border of the rostral is curved downward toward the tip. The dorsal profile of the nasals and of the crest is almost in line, the former being concave, as usual, as contrasted with the convex profile of *obtusus*. The orbit is an elongated ellipse, with the axis inclined at an angle of about 20 degrees from the perpendicular.

The infratemporal fossa [= fenestra] is of medium size, oval, with the apex pointing downward and forward. The nasal horn core is lacking entirely, the nasals rounding into the curve of the muzzle without a break in the even contour. The nasals terminate in a broad, rounded rugose area more suggestive of *Triceratops obtusus* than of any other form, and, as in the latter, they are twice as broad, at the rear as at the forward end.

The crest is broad, at least twice that of its length when viewed from above, and its dorsal profile is nearly straight without undulations, but with a slight upward turn toward the rear. — — — The number of epoccipitals is 19, 5 on each squamosal and 1 over the end of either squamosal-parietal suture, exactly as in *Triceratops*. The crest is highly vascular above and below with no limited zone on the inferior face." (Lull, 1933, p. 127.)

This was followed by a lengthy review of the crestal "fenestrations" and a repetition of his conclusion that these are all pathologic or due to injury, or both, and thus have no taxonomic significance. He concluded that *Diceratops* may be valid as a subgenus and the species he considered valid — a possible culmination of the evolutionary trend represented by *Triceratops obtusus*. Lull did not identify any other specimens, other than the type skull, that are referable to *T. hatcheri*.

It is our opinion that Lull was correct in his interpretation of most of these apparently anomalous "fenestrations" were due to injury, disease or preservation. While the anomalous "fenestrations" in the frill of U.S.N.M. 2412 seem to provide no reliable biologic information, the lateral temporal fenestrae here definitely do. As noted at several places in this section, the shape, size or orientation of the lateral fenestra have frequently been represented as specific characters. That claim is refuted by this specimen in which the left and right fenestrae are not at all like each other in shape or orientation, and are only approximately equal in size. So much for these "diagnostic" features.

Concerning the nasal knob or boss that first led to the suggestion of a distinct genus for this specimen, please see Part III.

TRICERATOPS INGENS Lull, 1915.

This "species" of *Triceratops* was mentioned by Lull (1915), apparently a working name of Marsh's, in his review of Cretaceous mammals and horned dinosaurs from the Lance formation of Niobrara County. The specimen consists of largely unprepared cranial and post-cranial material (Y.P.M. 1828) collected by Hatcher. No description of the specimen or diagnosis of the species were provided by Lull. Consequently, the species is not valid under the Rules of International Zoological Nomenclature and it is here recorded as an *Nomen nudum*. Until the specimen is further prepared, it is not yet even certain that it can be referred to *Triceratops*.

TRICERATOPS MAXIMUS Brown, 1933.

This species was established by Brown primarily because of the unusual size of the remains. The type specimen (A.M.N.H. 5040) consists of eight separate vertebrae and two anterior cervical ribs. These were collected from the Hell Creek formation in Garfield County, Montana. Although much was made by Brown of the significance of the great size of the individual represented by these remains, Brown's report gave only the absolute dimensions of the preserved elements with no comparative values for those of more normal sized individuals. Thus, from his paper, one cannot compare *T. maximus* with a "standard" size *Triceratops* species. Nor are any comparative illustrations or morphological comparisons of any significance. Comparison of dimensions of *T. maximus* with those of *T. brevicornis* indicate this specimen is approximately 50% larger than *T. brevicornis*, which could be taxonomically significant, but it might also be the result of age or individual variation. Brown dismisses sex as improbable. Brown gave the following specific characters:

"Axis rib reduced in size. Third cervical rib massive. Centra of free cervical vertebrae short, vertical and transverse diameters of articular faces nearly equal, sides deeply constricted, ventral surfaces flat. Anterior dorsal centra higher than broad." (Brown, 1933, p. 2.)

Of course these criteria are of no value in establishing a distinct species of *Triceratops*, because they apply to known cervical and dorsal vertebrae of other species of *Triceratops* which have been established on cranial criteria. Lull (1933) repeated Brown's characters, but observed that this species is not definable in terms of cranial criteria used in defining other species of the genus. Other comments by Lull are:

"A careful comparison of the description and dimensions given by Brown fails to distinguish the vertebrae from those of *Triceratops 'ingens'* (Y.P.M. 1828) in so far as equivalent bones are present in the two specimens, except that in certain dimensions cervical IV of *maximus* is a trifle larger, and the three equally spaced foramina on the side of the centrum are represented by one large one and others less clearly defined and not so regularly spaced." (Lull, 1933, p. 130.)

It is not evident why Brown referred this specimen to *Triceratops* since no skull material was recovered. Perhaps it was because of the stratigraphic occurrence, because vertebrae are not known for *Torosaurus*, the only other ceratopsian genus known from the Lance - Hell Creek section. Brown merely states:

"More characteristic parts of the skeleton, when discovered, may show that this species belongs to another genus, but until adequate material is secured it is referred to *Triceratops*." (Brown, 1933, p. 1.)

As things now stand, this specimen is not assignable to any genus and *T. maximus* must be considered a *Nomen dubium*.

TRICERATOPS EURYCEPHALUS Schlaikjer, 1935.

This species, based on a nearly complete skull and jaws and some skeletal fragments (M.C.Z. 1102), was collected from the Torrington member of the Lance formation of Goshen County, Wyoming, (NE 1/4 Sec. 4, T.22N., R. 61W.). The skull displayed distinctive features that convinced Schlaikjer it represented a new species. Schlaikjer listed those specific characters as follows:

- "1. Crest greatly expanded in proportion to the length of the skull.
2. Facial region abbreviated and broadly triangular in outline when seen from above.
3. Orbit elevated so that almost two-thirds of its area is above the posterior of the nasal.
4. Anteroinferior corner of the squamosal extended forward, giving a straight anterior border to the squamosal.
5. Dentary short and proportionately deep with high coronoid which distally is little antero-posteriorly expanded.
6. Brow horns proportionately very long and relatively slender.
7. Nasal horn greatly diminished.
8. Olfactory nerves separate and diverge laterally immediately in front of the cerebellum." (Schlaikjer, 1935, p. 55.)

This was followed by a detailed description of the skull and a lengthy discussion of the phylogenetic relationships and cranial morphologic patterns within the genus *Triceratops*. His conclusion was that:

TABLE 3: CEPHALIC INDICES OF SOME OF THE SPECIES OF *TRICERATOPS* (FROM SCHLAIKJER, 1935).

Species	Age	Skull Length	Skull Width	Index
<i>T. eurycephalus</i>	immature	138.6	129.7	93.5+
<i>T. calicornis</i>	not fully adult	210.0	155.2	73.9+
<i>T. elatus</i>	immature	193.4	?	?
<i>T. hatcheri</i>	old	185.4	132.8	71.6+
<i>T. brevicornis</i>	old	165.2	112.0	67.8+
<i>T. serratus</i>	immature	171.0	115.0	67.2+
<i>T. prorsus</i>	aged	152.3	94.4	61.9+
<i>T. flabellatus</i>	very young	187.9	86.4	45.9+
<i>T. horridus</i>	fully grown	?	?	?
<i>T. obtusus</i>	old	?	?	?

Schlaikjer's table showing eurycephalic (70.1-94+), mesaticephalic (65.1-70) and stenocephalic (40-65) cephalic indices of some of the species of *Triceratops*. Measurements are in cm.

"*Triceratops eurycephalus* is a very advanced species and it presents a culmination of the main evolutionary trends in *Triceratops* development during Lance times. Its phylogenetic position is somewhat intermediate between *T. hatcheri* and *T. calicornis* though it is nearer to the former. It aids greatly in determining the phylogeny of all the *Triceratops* species." (Schlaikjer, 1935, p. 65.)

Schlaikjer was impressed with the unusual width of the crest compared with the length of the skull, and indeed it is distinctive in this specimen. This is the primary reason for a new species and the specific name was well chosen. Comparing crest width/skull length ratio of *T. eurycephalus* with the same ratios in specimens (not designated) of six other species of *Triceratops*, Schlaikjer demonstrated that M.C.Z. 1102 has a proportionately wider crest than any other species measured. We are not sure what significance this has, but his results are repeated here. (Table 3)

It is unfortunate that Schlaikjer did not identify the specimens used in this analysis, or clearly define the dimensional vectors (ie, is the skull length the maximum distance between the rostral tip and the posterior edge of the frill, or is it the horizontal length?). Nevertheless, Schlaikjer provided a new cranial parameter of more than ordinary interest. He arbitrarily subdivided the range of cephalic indices found in *Triceratops* (see Table 3) into three categories — eurycephalic or "wide-headed" forms (*T. eurycephalus*, *T. calicornis* and *T. hatcheri*), mesaticephalic or "mid-width-headed" kinds (*T. brevicornis* and *T. serratus*) and stenocephalic or "narrow-headed" varieties (*T. prorsus* and *T. flabellatus*). Notice in Table 3 that both young and old individuals are represented in each category.

As mentioned earlier, we do not understand the biologic (or taxonomic) meaning of this phenomenon even though Schlaikjer observed that it is an ontogenetic expansion of crest width (enlargement of the parietals and squamosals) irregardless of antorbital and/or postorbital skull growth. He demonstrated this by comparing an immature *Protoaceratops* specimen (A.M.N.H. 6408) with an adult specimen (A.M.N.H. 6414) where the crest width was 260 mm greater in the adult compared to a greater skull length of just 209 mm. According to that, we should expect the youngest specimens to be stenocephalic (notice *T. flabellatus* in Table 3) and the oldest to be eurycephalic. Of the eurycephalic specimens in Schlaikjer's table only one of the three has been judged to have been an old individual, and the "aged" specimen of *T. prorsus* shows a stenocephalic condition!

TRICERATOPS ALBERTENSIS Sternberg, 1949.

As of this writing, this is the last named species of *Triceratops*. It was proposed by C.M. Sternberg for a fragmentary specimen collected from the Upper member of the Edmonton formation at a site not far from Drumheller, Alberta (NW 1/4 sec. 2, Township 34 N. Range 22 W, 4th Meridian). The specimen (G.S.C. 8862) consists of an incomplete left half of a large skull, now in the Canadian Geological Survey collections in Ottawa, Ontario. The skull lacks the beak and nasal horn core, the parietals, quadrate and entire right side. Consequently, the estimated skull length of at least 8 feet cannot be verified. The total preserved length is 1.93 m.

Sternberg (1949) listed the specific characters as follows:

"Large form; facial region high, long, massive; antorbital fossa large; orbit large, higher than long, top well above nasals and frontals; brow horn core large, mostly behind orbit, flattened externally, tapering, and standing erect or slightly backward; jugal long and heavy with epijugal; squamosal long, thick with epoccipitals and vascular markings on both sides; crest large, gently rounded, and not strongly upturned behind; vertebrae and ribs massive."

Sternberg continued with:

"The specimen differs from all other species of *Triceratops*, but appears to most nearly resemble the skull of *T. horridus*. The anterior edge of the nasal, as preserved, is 80 mm thick. It is slightly upturned and suggests that it was thickened for a nasal horn core, which was, no doubt, formed by an upgrowth of the nasal bone. The nasals and frontals are broad and the top of the head is gently rounded. The face, or that part between the orbit and the nasal excavations, is longer than in *T. horridus*. — — — An outstanding feature of our new species is the exceptionally large preorbital fossa [= lachrymal foramen?], which is larger than in any other known ceratopsian. It is subcircular in outline and is situated far forward. The bones of the skull are so thoroughly ossified that it is not possible to state what bones bound the fossa. — — — The orbit extends well above the top of the nasal bones. It is oval in outline, with the base of the oval at the antero-inferior angle and the long axis inclined more than 15 degrees from the perpendicular. — — —

The brow horn core is very broad-based and the fore and aft diameter is considerably greater than the transverse diameter. It stands well behind the orbit and is directed posterior to the perpendicular. As the skull was preserved on its side, the angle of the horn could not be due to distortion. As in other species of the genus, the horn core is hollow in its lower half and the walls are relatively thin. — — — It is uniformly tapered and the top, as preserved, is 720 mm above the level of the orbit. Vascular markings are well shown, but not particularly deep. — — —

The jugal is large and the long descending limb slopes slightly backward. — — — There is no sharp ridge on the external face of the jugal, which is gently rounded toward the distal end. A well-pronounced, blunt epijugal is thoroughly fused to the inferoexternal edge. The quadratojugal and quadrate are not preserved and the lateral temporal fossa is not enclosed. — — — The jugal notch is moderately deep but broad. — — —

The squamosal is long and of moderate breadth. It is rounded laterally and posteriorly it gradually flattens out, suggesting that the crest was not upturned posteriorly. Both upper and lower surfaces are marked with vascular grooves though they are not extremely deep except on the external face of the antero-inferior part. There are seven low, epoccipitals thoroughly fused to the edge of the squamosal. In general shape and proportions, the squamosal is intermediate between that of *T. eurycephalus* (12, Pl.4) and *T. flabellatus* (7, Pl.44) though the jugal notch is more like that of the latter. The angle of the internal edge of the squamosal suggests that the parietals were not particularly broad behind but rather that the crest was long but of moderate breadth." (Sternberg, 1949, pp. 38–40.)

Several points here (marked by , ,) are worth some comment. First of all, it appears to us that this specimen has not been correctly oriented and as a consequence, several features present peculiar orientations. For example, Sternberg describes the crest as "not strongly upturned behind" and illustrates it as a curved but nearly horizontal frill. Also, he notes that brow horns are erect or project slightly backward. If correct, that would be the only occurrence among all ceratopsians. As recorded, the ventral margin of the left, and only preserved, maxilla is not preserved, so there is no datum or "horizontal" reference plane. The absence of the snout does not help matters. If this skull were tilted 15 or 20 degrees downward at the front, the crest would have a more typical ascending profile and the brow horns, while still erect, would

project forward rather than backward. Such tilting would reorient the orbit from a forward inclination of more than "15 degrees from the perpendicular" to a nearly vertical position as in *T. prorsus* and *T. calicornis*, and more like the less-than-15-degree angulation of the orbit in *T. brevicornis* and *T. elatus*. Such manipulation of the skull is essential because we are dealing with orientations of "diagnostic" features with reference to absolute data — horizontal and vertical. The result of our manipulation is a skull profile that is more like those of other *Triceratops* specimens. It satisfies the curious condition of backwardly directed brow horns, a condition not known in any other ceratopsian to our knowledge.

On another point, in the absence of a complete snout and nasal horn, the upturned and "thickened" anterior end of the nasals may suggest the original presence of a nasal horn, but that condition is not known — and considering the state of *T. obtusus* and *T. hatcheri*, we must be very cautious. We do not know whether a nasal horn ever existed in this specimen, so

we cannot make "suggestions" that might be interpreted as supportive evidence for a particular taxonomic assignment.

With these several points in mind, together with the very incomplete condition of the type skull, our conclusion is that this specimen cannot be assigned with confidence to any species of *Triceratops*. (In fact, one could argue that it cannot even be assigned with certainty to this genus.) We believe this species to be inadequately founded, but consider it to be a probable synonym of *T. horridus*.

— — —

For the sake of completeness, it must be recorded here that Kuhn, in *Fossilium Catalogus* (1936) listed as questionable species of *Triceratops*, *T. sylvestris* [type species of *Agathau-mus* by Cope, 1872] and *T. mortuarius* [type species of *Polyo-nax* by Cope, 1874]. These referrals were repeated by Kuhn in the 1964 Supplement I of *Fossilium Catalogus*. Since the type specimens of these two species include no diagnostic cranial material, they are not referable to the genus *Triceratops*.

TRICERATOPS SPECIES SUMMATION: ORIGINAL DISTINGUISHING FEATURES

Triceratops alticornis: A pair of long and elevated frontal horn cores with slender pointed ends and basal cavities.

Triceratops horridus: Skull bearing much larger frontal horns than in any other known animal, living or extinct.

Triceratops flabellatus: Larger skull with a long occipital crest extending up and backward, like a fan, with its posterior margin armed with a row of horny spikes on separate ossifications.

Triceratops galeus: A much smaller species with a nasal horn compressed longitudinally, apex is pointed and directed well forward and the horn is coossified with the extremity of the nasals.

Triceratops serratus: The occipital crest features a series of bony projections along the crest mid-line.

Triceratops prorsus: The nasal horn core is very large and is directed straight forward.

Triceratops sulcatus: Large and elongate frontal horn cores which feature deep grooves on the posterior surface of the upper half of the horns.

Triceratops elatus: Skull with an elongate and much elevated parietal crest.

Triceratops calicornis: The nasal horn core is directed well forward, and unlike any other known, is concave above, with the upper or posterior surface resembling the underside of "a horse's hoof".

Triceratops obtusus: The nasal horn core is very short, only about one inch long, obtuse and rounded.

Triceratops brevicornis: Both the frontal and nasal horn cores are short and stout.

Triceratops hatcheri: Frontal or supraorbital horn cores short and robust, nasal horn core absent.

Triceratops ingens: (No description ever given.)

Triceratops maximus: Distinguished on the basis of the large size of the vertebrae — 30 to 50% larger than other described species. (Generic assignment in doubt.)

Triceratops eurycephalus: Occipital crest proportionately wider relative to skull length than in any other species of *Triceratops*.

Triceratops albertensis: Antorbital fossa very large and brow or frontal horns directed vertically or backward.

Summary of the kinds of anatomical features and conditions present or absent in numerous skulls of *Triceratops* that were seen as important taxonomic characters by previous workers. The number of specimens involved ranges from one (in *T. albertensis*, *T. galeus*, *T. alticornis* and others, to as many as six or more in *T. elatus*). Readers are invited to draw their own conclusions. A number by a marked character designates the author(s) of this supposed diagnostic character. 1 = Marsh, 2 = Hatcher, 3 = Lull, 4 = Brown, 5 = Schlaikjer, 6 = Sternberg, 7 = Gilmore.

TABLE 4: TAXONOMIC DISTRIBUTION OF *TRICERATOPS* CHARACTERS
REPORTED BY PREVIOUS WORKERS

CHARACTERS TRICERATOPS "SPECIES"	<i>T. alticornus</i>	<i>T. horridus</i>	<i>T. flabellatus</i>	<i>T. galeus</i>	<i>T. serratus</i>	<i>T. prosus</i>	<i>T. sulcatus</i>	<i>T. elatus</i>	<i>T. callicornis</i>	<i>T. obtusus</i>	<i>T. brevicornus</i>	<i>T. hatcheri</i>	<i>T. ingens</i>	<i>T. maximus</i>	<i>T. eurycephalus</i>	<i>T. albertensis</i>
Brow horns grooved							•1									
Brow horns short																
Brow horns long	•1	•1,3	•1				•1	•1,3	•3		•2	•2			•5	•6
Brow horns curve up then forward		•3	•		•	•2,3		•1,3	•3	•	•	•				
Brow horns curve sharply forward								•1,3	•							•6
Brow horns vertical or backward								•3	•		•2	•2				
Brow horns massive, robust		•1,3						•3	•		•2	•2				
Brow horns slender	•1				•2,3	•2,3		•3	•						•5	
Brow horn basal section oval		•			•3			•1,3				•2				•6
Brow horn basal section circular			•									•2				
Nasal horn absent					"•"1					•?		•2				
Nasal horn concave above									•1							
Nasal horn short	•2	•	•				•	•2,3	•3	•1,2	•2				•5	
Nasal horn long						•2,3				•3,7						
Nasal horn directed upward	•1					•1,2		•1,2								
Nasal horn directed forward				•1		•3										
Rostral small					•							•2				
Rostral large, heavy		•3						•3	•3			•3				
Rostral lower margin straight					•											
Rostral lower margin sharp			•1		•	•2,3			•							
Rostral lower margin dull	•	•														
Rostral tip strongly downturned	•				•											
Rostral deeply excavated beneath											•3					
Muzzle short		•				•3										
Muzzle long	•				•				•3							
External nares very large									•3							
Face long					•	•										
Orbit round						•1	•2									
Orbit oval, inclined 15 degrees	•							•3	•3			•				•6
Orbit oval, inclined 30 degrees											•1					
Orbit oval, inclined 45 degrees			•		•3	•3										•6
Orbit large								•2								
Interorbital area concave												•2				
Interorbital area convex	•1															
Lachrymal foramen in maxilla						•2,3	•2,3									
Lach. for. at max.- nasal suture		•2			•2,3	•2			•		•?3					•6
Lachrymal foramen very large																
Infratemp. fenest. large, quadr.					•											
Infratemp. fen. triang. rear apex											•					
Infratemp. fen. triang. apex down								•								
Infratemp. fen. triang. apex forw.						•										
Infratemp. fen. oval, inclined		•							•3							
Infratemp. fen. oval, not inclined					•2							•				
Jugal process stout	•	•														•6
Jugal process narrow						•3		•								
Jugal process tapered						•3			•							•
Jugal process inclined backward						•3		•2								
Jugal process inclined forward												•				
Jugal process vertical	•				•				•							•
Jugal process with median ridge	•				•	•2		•3	•	•	•					•
Jugal notch deep	•								•	•						
Jugal notch shallow									•	•						
Jugal notch wide									•2							
Jugal 7-shaped																
Epijugals present		•					•				•?					•6
Parietal crest long								•1								•
Parietal crest wide					•							•			•5	
Crest directed mostly backward								•1								•
Crest directed strongly upward		•1									•3					•
Crest with dorsal vascular marks	•								•	•		•				•
Crest with ventral vascular marks					•1	•2				•						•
Crest with mid-line prominences																
Squamosal prominences at horn base					•1			•3	•?3	•?3						
Epoccipitals present		•1	•		•				•	•?	•	•				•
Epoccipitals - 19		•							•?3		•3	•				
Epoccipitals - 17					•											
Epoccipitals - 15						•2										
Epoccipitals - 14						•?		•								
Postfrontal fontanelle present									•		•2	•				
Postfrontal fontanelle closed						•2										
Mandible slender		•			•	•3										
Mandible deep, robust									•	•2,3	•				•5	
Coronoid process expanded distally		•			•	•3						•				

SUMMARY OF NAMED SPECIES

From the preceeding review of the taxonomic history of the species of *Triceratops*, too many species have been established on inadequate material or doubtful criteria, as several previous authors have observed. At least five or these taxa must be abandoned on technical grounds:

1. *T. alticornus* – Nomen dubium. Based on completely inadequate material, that cannot be assigned to any genus. Ceratopsian remains of indeterminate affinity.

2. *T. galeus* – Nomen dubium. Based on totally inadequate remains of indeterminate ceratopsian identity.

3. *T. sulcatus* – Nomen dubium. Distinctive “unique” feature is highly variable and no other feature distinguishes this taxon from other species of *Triceratops*.

4. *T. ingens* – Nomen nudum. The name was published without either diagnosis or description.

5. *T. maximus* – Nomen dubium. Based on inadequate material. The taxon is ceratopsian, may be unique, but is not presently assignable to any genus.

In addition, two more species of *Triceratops* must be considered doubtful.

6. *T. obtusus* – Originally based on insufficient cranial material, subsequent study of the nearly complete skull by Gilmore (1919) failed to detect any characters that distinguish this taxon from previously named species. We concur. The short nasal horn core probably reflects a highly variable feature. The type specimen appears most similar to *T. horridus*.

7. *T. albertensis* – With the exception of the large antorbital fenestra, the most distinctive features (vertical or backwardly projecting brow horns and the low, non-upturned crest) appear to be mis-interpretations resulting from mis-orientation of the skull due to the absence of any preserved reference datum to the horizontal or vertical. Most probably a synonym of *T. horridus*.

28. While the species may be valid, we must point out that, as preserved, the type specimen of *hatcheri* lacks a definitive character of the genus *Triceratops* – the nasal horn core.

This reduces the roster of *Triceratops* species to the following:

T. horridus
T. flabellatus
T. serratus
T. prorsus
T. elatus
T. calicornis
T. brevicornis
 ? *T. hatcheri*
T. eurycephalus

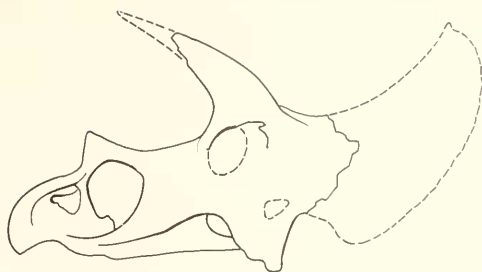
These “surviving” taxa appear to have been founded on adequate material, and presented with sufficient description and documentation, and therefore are retained on technical grounds. Whether in fact, each represents a true species cannot be tested on the anatomical evidence available. What is unacceptable as a valid species character to one taxonomist may be entirely acceptable to another. Certainly the forwardly directed nasal horn of *T. prorsus* is distinctive, but is it a specific difference? The wider frill relative to skull length of *T. eurycephalus* is unique among these taxa, but why is that a taxonomic difference rather than an individual variable or a sex difference? (See also Dodson, 1976.)

We have no intention of evaluating the taxonomic worth of the various features that have been cited in these specimens. Any judgement by us as to the meaning of horn length or curvature, or frill length or width etc. would be arbitrary – and all contrary judgements would have equal merit. Having presented the historical record and summarized the surviving assemblage of *Triceratops* species, we now turn to another approach.

Fig. 9: *Triceratops* type skulls originally assigned to different species, but according to the systematic revision presented in this paper (see p. 156) taken to be synonyms of the valid species *T. horridus* Marsh, 1889. The line drawings are reduced to the same scale and based on the illustrations published: *T. prorsus*, Y.P.M. 1822 (Hatcher et al. 1907, p. 34), Niobrara County, site 3 on map, figure 15. *T. horridus*, Y.P.M. 1820 (Hatcher et al. 1907, pl. 26), Niobrara County, site 1 on map, figure 15. *T. serratus*, Y.P.M. 1823 (Hatcher et al. 1907, pl. 27), Niobrara County, site 4 on map, figure 15. *T. elatus*, U.S.N.M. 1201 (Hatcher et al. 1907, pl. 43), Niobrara County, site 16 on map, figure 15. *T. brevicornis*, Y.P.M. 1834 – now B.S.P. 1964 I 458, Niobrara County, site 22 on map, figure 15. *T. hatcheri*, U.S.N.M. 2412 (Hatcher 1905, pl. 13, fig. 1), Niobrara County, site 25 on map, figure 15. *T. flabellatus*, Y.P.M. 1821 (Hatcher et al. 1907, pl. 44), Niobrara County, site 2 on map, figure 15. *T. calicornis*, U.S.N.M. 4928 (Hatcher et al. 1907, pl. 38), Niobrara County, site 29 on map, figure 15. *T. eurycephalus*, M.C.Z. 1102 (Schlaikjer 1935, fig. 3), Goshen County, Wyoming. The differences in the robustness of the horn cores could be an indication of sexual dimorphism.



Tr. prorsus



Tr. horridus



Tr. serratus



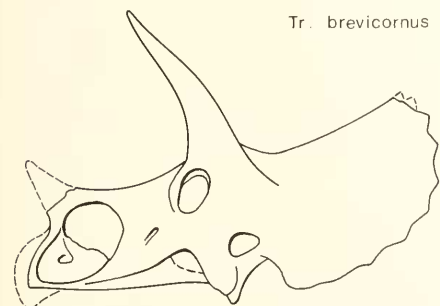
Tr. elatus



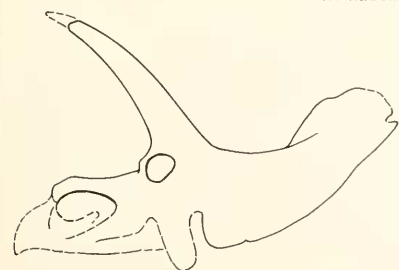
Tr. brevicornus



Tr. hatcheri



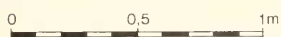
Tr. flabellatus



Tr. eurycephalus



Tr. calicornis



PART III: SYSTEMATIC PROBLEMS AND A REVISION OF THE GENUS

INTRODUCTION

Species are, and always have been defined or diagnosed on the bases of several kinds of criteria. Unique anatomical features and morphologic differences are foremost among these. But physiologic, biochemical, even geographic and behavioral observations (and others) of living organisms provide other (sometimes non-diagnostic) characteristics by which we recognize or describe different kinds. Because we are not

able to apply to fossil material most of these other measures or tests that are available to neo-taxonomists and zoologists, it is important, indeed essential, that we premise all paleo-taxonomy on well-established neo-zoologic foundations and thinking — zoogeography, faunal composition, population structure, ecology and animal behavior, as well as anatomical variation and the sources of such variation.

TAXONOMIC CRITERIA AND THE SOURCES OF ANATOMICAL VARIATION

The single greatest source of frustration in taxonomic studies of fossil organisms is morphologic variation and its causes. Yet, in the absence of any other taxonomic criteria, we are dependent on morphologic differences in distinguishing between different taxa. Our assumption is that such anatomical differences reflect genetic distinction. Unhappily, that assumption cannot be tested. And even though everyone knows that there will be anatomical differences between any two individuals, a long-standing paleontological tradition emphasizes these differences in establishing new taxa while under-rating morphologic similarities.

Although known to every reader, it is necessary here that we be reminded of the kinds or sources of anatomical variation. That is not because we can distinguish them in a fossil assemblage with any degree of confidence — but so we are cognizant of the difficult, if not insoluble problem involved. Briefly, anatomic diversity is the result of taxonomic difference, ontogenetic age, sexual difference or simply individual variation. Without a large sample, one can never be confident which of these sources is responsible for the variation observed. Obviously, at least three of these may be represented in any population sample and all four could be involved in any fossil assemblage. Selecting the “correct” anatomical character(s) that represent specific or generic distinction of fossil material has always been pretty much a matter of taste. It hardly could be otherwise, when we have no true measure of the variability within the original population, our sample sizes are usually insufficient to distinguish between sexes, and rarely is an unmistakable growth series at hand.

To illustrate our point, the “sample” we concerned ourselves with consists of the type specimens of *Triceratops* collected from a local geographic region. We have assumed that this “sample” includes both sexes (see next section, p. 153). Figure 9 illustrates in profile most of those type skulls. We suspect that the apparent robust vs. slender form of the brow horn-cores reflects sex differences, but it could just as well be individual variation. Taxonomic difference seems unlikely.

In the present case, sixteen species have been named and placed in the genus *Triceratops*. Five of these have subsequently been considered inadequately or improperly founded by either Hatcher or Lull. Gilmore (1919) expressed his views on the situation as follows:

“In the present accepted classification of the Ceratopsia, and especially of the genus *Triceratops*, great importance is attached to the development of the nasal and supraorbital horn cores, and the peripheral outgrowths of the frill. It is not yet clear how much dependence can be placed on the differences found in these horns, or their almost complete absence as in *T. obtusus*. There is great variation, as might well be expected in such highly specialized outgrowth, and the differences in sex, and stage of growth present other features that have also to be considered before a satisfactory conclusion can be reached as to what characters constitute valid specific differences. — — — At the present time it appears quite certain that the number of described species is too great by a considerable number.” (Gilmore, 1919, pp. 100–101.)

Reflecting on Gilmore’s assessment, and after consideration of the indeterminate sources of anatomical variation that are responsible for the diversity represented in the type specimens of the many *Triceratops* “species”, it is appropriate to refer back to the Table of anatomical conditions (Table 4) and the summary (pp. 144–145) of the original distinguishing characters that persuaded the six authors to propose the sixteen named species of *Triceratops*. There is no method or logic by which we can confirm or refute the taxonomic validity of any of those anatomical differences, prominent or subtle as they may be.

That being the case, we have only one direction to turn — to living examples as possible approximate analogues. Consider the life size of the adult *Triceratops* — up to six metric tons, and possibly as much as eight tons, and nearly 10 meters in length. Today, of course, there are only two terrestrial species that come close to that size — *Loxodonta africana* (ca. 7 to 8 metric tons) and *Elephas maximus* (ca. 5 tons). Morphologically distinct, yet there are no anatomical variation studies for either. The two species are not sympatric.

Next smallest of living terrestrial animals are the Rhinocerotidae, of which there are five species assigned to four genera. Again, the anatomical differences are notable, but no va-

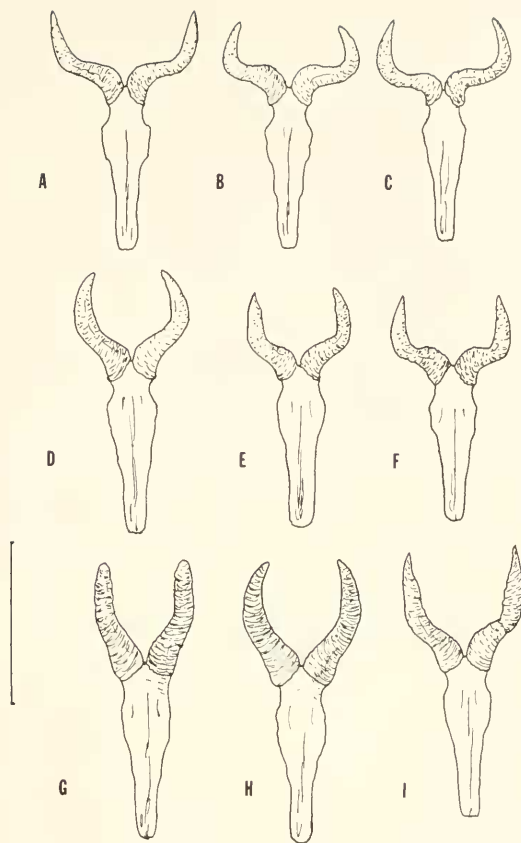


Fig. 10: Examples of horn variation in *Alcelaphus buselaphus* (Hartebeest) of central Africa. The series was selected from different locales within the normal range of the species by Ruxton and Schwarz to demonstrate hybridization between two subspecies of *A. buselaphus* — *A. b. jacksoni* and *A. b. cokii*. Scale equals 40 cm.

- A. = *Alcelaphus buselaphus jacksoni*, Lake Nakuro, Kenya.
- B. = *A. b. jacksoni*, Lake Naivasha, Kenya.
- C. = *A. b. cokii*, Mlali Plain, Tanganyika.
- D. = *A. b. jacksoni*, Lake Nakuro, Kenya.
- E. = *A. b. jacksoni*, Guas Ngishu Plateau, Kenya.
- F. = *A. b. jacksoni*, Lake Nakuro, Kenya.
- G. = *A. b. lelwel*, Bahr et Ghazal, Kenya.
- H. = *A. b. jacksoni*, Ongotto Nairowa, Kenya.
- I. = *A. b. jacksoni*, Njoro, Kenya.

Redrawn from Ruxton and Schwarz, 1929.

riation studies are available. No two species are now sympatric, although the African species *Diceros bicornis* (ca. 1 to 1.8 metric tons) and *Ceratotherium simum* (ca. 2.3 to 3.6 tons) probably were. *Rhinoceros sondaicus* (ca. 3 metric tons) and *Didermoceros sumatrensis* (ca. 1 ton), the Asian and Sumatran rhinos, may also have had overlapping ranges in the past.

Further down the animal-size scale is the giraffe family — *Giraffa camelopardalis* (1800 kg.) of southern Africa and *Okapi johnstoni* (250 to 300 kg.) of the Congo region. No

studies on variability of either species is known to us. They are not sympatric.

The family Bovidae is in some respects perhaps the best living ceratops analogue, although ceratopsians are most frequently compared with rhinos. The water buffalo *Bubalus bubalis* (800+ kg.), the American buffalo *Bison bison* (1300 kg.), the African buffalo *Syncerus caffer* (900 kg.) and common cattle and variants *Bos taurus* (900+ kg.) are all considerably smaller than any known adult specimen of *Tricera-*

tops, but should be included here. Variation studies are not available for most, but the variability of *Bos* is common knowledge. Some zoologists recognize fewer or more distinct species of some of these genera (i.e. *Bos taurus*, *B. indicus*, *B. gaurus*, *B. frontalis*, *B. bantung*, etc. and *Syncerus caffer* or *S. nanus*), but no hybridization data are available for most (but see Grubb, 1972). Intra-specific variation data likewise are scant. With the exception of *Bos taurus* (the geographic distribution of which is virtually cosmopolitan), there are no variation statistics known to us on the other above mentioned bovines. *Bubalus*, *Bison* and *Syncerus* are morphologically and geographically distinct. The various "species" of *Bos* (together

with the several domesticated varieties) provide some insight about the degree of variability within a large terrestrial herbivore "species complex". In this case, horn variability is well known, even if not statistically documented. Figures 10 and 11 illustrate some examples of these.

It is not our intention to include a detailed study of comparative variation among bovine species, only to draw the readers' attention to the fact that considerable variation does occur, particularly in horn size and shape. Also, we note the allopatric distribution of certain closely related large mammalian herbivores today. The analogy cannot be overlooked.

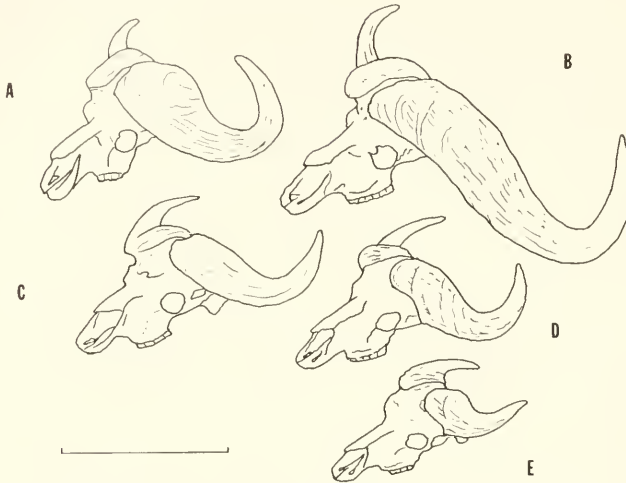


Fig. 11: Intra-specific variation in the skulls and horns of *Syncerus caffer caffer*, the African forest and savanna buffalo, to show hybridization and "incipient" speciation. Scale equals 50 cm.

- A. = *Syncerus caffer caffer*, Mt. Elgon, Uganda.
- B. = *S. c. caffer*, Amala River, Kenya.
- C. = *S. c. cottoni*, Kasindi, Lake Edward, Congo Kinshasa.
- D. = *S. c. mathewsi*, Mfumbiro, Ruanda.
- E. = *S. c. nanus*, Ituri Forest, Congo Kinshasa.

From Grubb, 1972.

VARIABILITY IN SOME MODERN SPECIES: HORNS — ARTIODACTYL VS. CERATOPSIAN

There is no need (or space) here to cite the numerous studies of variation in different living species. We include only two figures to reinforce what all readers know. For obvious reasons we chose horned "analogues". No statistical data are necessary — the visual evidence is sufficient. Our "sample" here was selected randomly — perhaps even as randomly as the *Triceratops* sample recovered by Hatcher from his Wyoming excavations.

Horns are the most distinctive ceratopsian feature. Horns have been the dominant character in all taxonomic statements since Marsh's original mis-conceived *Bison alticornus* (1887) paper. A comparison with the horns of artiodactyls in gene-

ral, and bovids in particular, is to be expected. The remarks that follow are therefore quite appropriate, even if not definitive.

Geist (1966) summarized horn evolution and function (in mammals) in an excellent paper, suggesting that horn-like features evolved independently several times, probably when creatures "discovered" that a head blow was an effective mode of fighting (defensive or otherwise). Increased mass and inertia of the head (certainly true of all ceratopsians) possibly led to development of cranial protuberances, which became enlarged and more complex as defensive adaptations (thick skin, bony armor, head shields or avoidance behavior) evol-

ved concurrently. The probable adaptive function of horns in ceratopsians has been explored by several authors, most recently by Farlow and Dodson (1975) and Farlow (1976).

We find the horn "classification" by Bruhin (1953) to be most useful in considering ceratopsian horns. The usual distinction between horns (permanent cranial out-growths) and antlers (cranial out-growths that are shed and regrown annually) is obvious. Since ceratopsian "horns" appear to have been permanent and bi-sexual features, the classification of Bruhin has particular significance. Accordingly, horn-like structures can be categorized as follows:

- 1) Horns that are similar in shape and size in both sexes. These function mainly as weapons against enemies, especially against predators. Examples: *Oryx*, *Hippotragus*, *Bison*.
- 2) Horns that appear to be useless against predators and function only in intra-specific combat. Examples: *Aepyceiros*, *Cobus* and *Redunca*. In this category, horns are sexually dimorphic or present only in the males.
- 3) Horns that are never used as weapons, but seem to have a signal or ceremonial function. Example: *Giraffa*.

In this classification, it is obvious that *Triceratops* (and ceratopsians in general) belong to the first category since no Late Cretaceous hornless ceratopsians have yet been discovered. Of course it is quite possible that the horns of *Triceratops* also functioned as display structures (sexual as well as defensive), but we have no way to test this.

The origin and growth of ceratopsian horns are also beyond test, yet there are a few clues. Brown and Schlaikjer (1940a) considered the matter, but seem to have generated no clear acceptance or rejection. They concluded that the brow-horn cores were formed by outgrowths of the postfrontal bones, citing (among others) an immature specimen of "*Triceratops*" (A.M.N.H. 5006). We find no evidence to challenge their conclusion and the lack of any evidence of sutures at horn bases supports their interpretation. *Triceratops* brow horns appear to have been comparable to bovid "brow horns" at least in their development and function.

The nasal horn of *Triceratops* appears to be another matter, though. Brown and Schlaikjer (1940a) argued that the distinct nasal horn was suturally united with the underlying nasal bones, (and thus an ontogenetically separate ossification). Again, we agree with their conclusion, and we cite the following:

- 1) The various isolated "nasal-horn cores", some of which preserve unquestionable basal suture surfaces (A.M.N.H. 5883, U.S.N.M. 4286 and the holotype specimen of *Triceratops galeus*, U.S.N.M. 2410).
- 2) The existence of several "*Triceratops*" specimens that feature nasal "bumps", rather than horns, such as U.S.N.M. 4720 (which has been referred to *T. obtusus*), U.S.N.M. 2100 (Hatcher's skull nr. 26 assigned to *T. elatus*) and the holotype of *T. hatcheri* (U.S.N.M. 2412) originally designated *Diceratops* because there is no nasal horn. Instead there is a long and rather broad nasal boss or convexity. Might not this nasal bone boss have provided a solid foundation for a true horn (as in the modern rhinoceros)? (See Lull, 1905.)
- 3) The most conclusive evidence, in our opinion, is preserved in the holotype of *Triceratops calicornis* (U.S.N.M. 4928).

Here, it is evident that there is an elongated dorsal "bump" on the nasal bones. Perched on top of the front part of this "bump" is the "nasal horn", but it has a peculiar shape. It is apparently separated from the nasals beneath by what appears to be a suture zone. The "horn" is symmetrical and unpaired, appears to "clasp" the underlying nasal boss from the front, and displays a unique concave posterior surface. This latter is what led Marsh (1898) to separate this specimen from his earlier species. He created a new species *T. calicornis* in reference to this peculiar shape of the nasal horn.

We interpret this last specimen (U.S.N.M. 4928) as the best evidence available that the nasal horn of *Triceratops*, unlike the brow horns, developed as a separate epidermal ossification supported by a prominent expansion of the nasal bones beneath. Figure 12 portrays this evidence. That mode of horn development is reminiscent of the development of horns in living bovids where the horns begin as dermal ossicones separate from the skull bones. The ossicones grow into the horn cores which very early in life fuse to the frontals (Bruhin, 1953; Gijzen, 1959). The horn core is covered by a mass of horn or cornified tissue. Relatively little is known about the development or growth-regulating mechanism of bovid horns, but it appears that the overlying cornified tissue is largely responsible for the great variety of horn types (Bruhin, 1953). In some bovids, horns reach their definitive size and shape early in life, after which there is little further growth (*Gorgon*, *Ovibos*). In other species, there is periodic or annual growth throughout life (*Ovis*, *Rupicapra*), probably related to cycles of sex hormone production.

Whether the bovid model is applicable to the ceratopsian horn development question is beyond demonstration. Certainly, the rugose and vascular-channeled surfaces of both brow and nasal horns indicate some kind of surficial covering, probably a horn or keratinized sheath like that of living bovids. The ceratopsian horns were permanent and borne by both sexes and probably were primarily defensive structures.

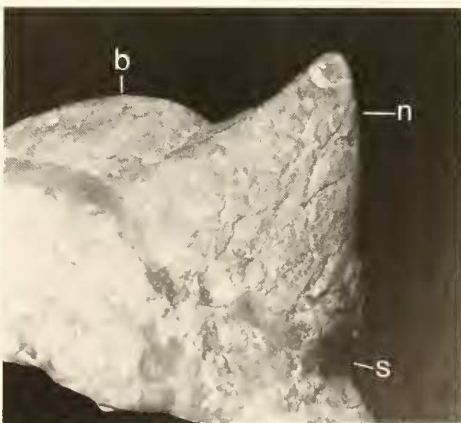


Fig. 12: The nasal horn core (n) of the type specimen of *Triceratops calicornis* (U.S.N.M. 4928) separated from the nasals beneath by a suture zone (s). Please notice the elongated dorsal "bump" (b) behind the horn core. Photograph courtesy of K. Carpenter, Univ. Colorado.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION OF *TRICERATOPS* SPECIES

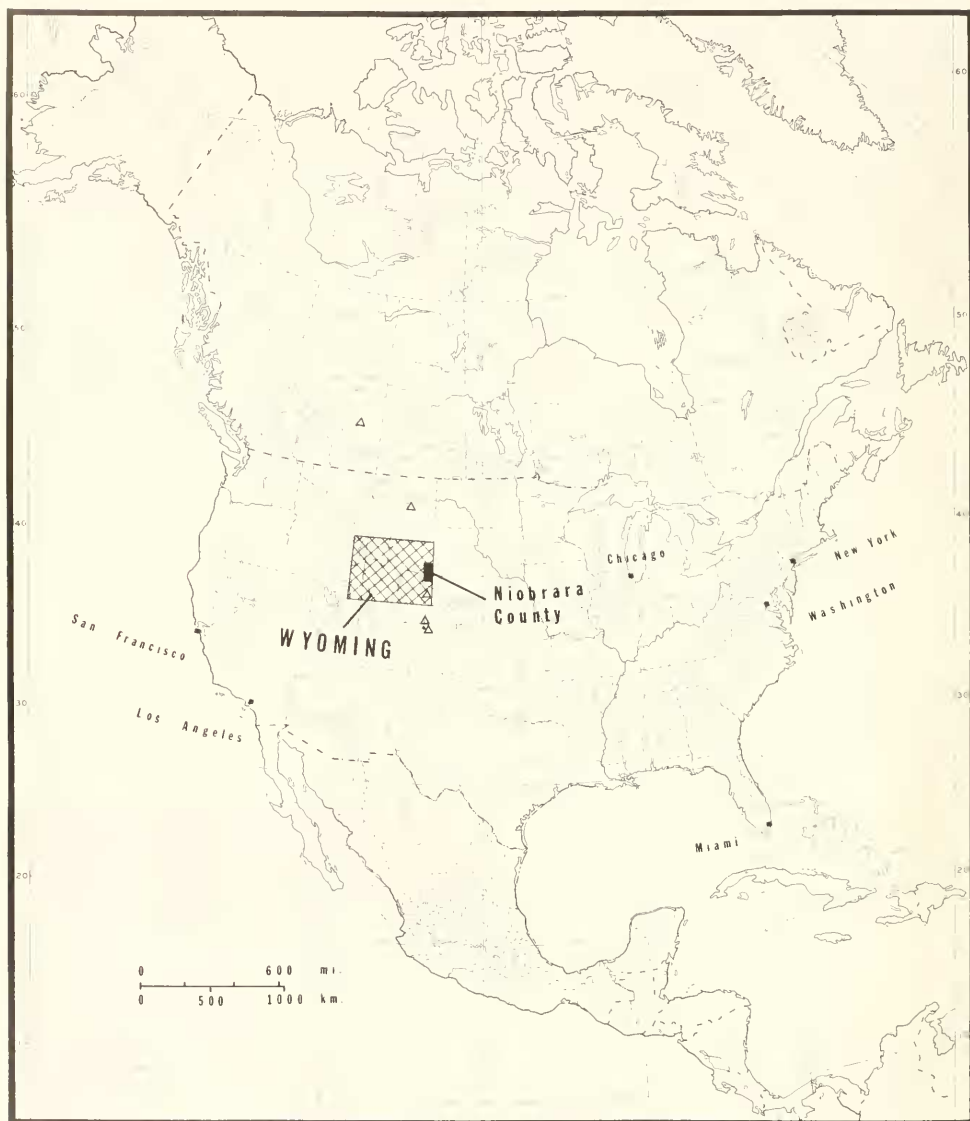


Fig. 13: Nearly all of the holotype specimens and most of the other early classic specimens of *Triceratops* were discovered in eastern Wyoming, in Niobrara County. Niobrara County is marked here by the black rectangle to show its size relative to North America. The open triangles indicate the approximate locations of the sites of the type specimens of the few other "species" of *Triceratops* that occur outside of Niobrara County. From south to north, these are the sites of: *T. alticornis* (U.S.N.M. 1871 e); *T. galeus* (U.S.N.M. 2410); *T. "eurocephalus"* (M.C.Z. 1102); *T. maximus* (A.M.N.H. 5040) and *T. albertensis* (G.S.C. 8862).

Since it does not appear possible to judge the validity of the several species of *Triceratops* on the merits of individual cranial "distinctions", we have chosen to look at some of the other evidence available and relevant, and to consider that evidence in the light of knowledge of modern biology.

Geographic Occurrence

It has not been possible for us to determine the exact site and stratigraphic occurrence of all specimens that have been attributed to *Triceratops*, but we have made a serious effort. That information is summarized in Table 1. All readers must understand that we have not validated the assignment to *Triceratops* in all instances, but we have excluded some specimens which we considered doubtful or indeterminate. The distribution of those specimens is interesting.

Now, if one compares this with the geographic distribution of the type specimens of *Triceratops* (Figs. 13–15) the picture becomes even more interesting. Only those of *T. albertensis* (a doubtful taxon) and *T. eurycephalus* stand out as lonesome occurrences removed from all the others. The close proximity of all these specimens within such a restricted geographic area can be explained very easily if we assume they

all belonged to the same species. But we have been told that they represent different species! That is not consistent with what we know about living species of large terrestrial animals. It is our view that all those type specimens from the Niobrara County sites that are clearly referable to *Triceratops*, belonged to a single species.

Stratigraphic Occurrence

Critics will immediately take exception to our conclusion, most probably on the grounds that these type specimens were not all recovered from the same stratigraphic level within the Lance formation. Our response to that is that available records clearly show that all but two of these type specimens were recovered from a restricted stratigraphic range. According to the stratigraphic occurrence of the Niobrara County *Triceratops* skulls published by Lull (1915, p. 343.), the type (Munich) specimen of *Triceratops brevicornus* was recovered from the highest stratigraphic level of all of the *Triceratops* type specimens obtained. It is noted there that Stanton (1909) observed that the skull (field number 22) of *T. brevicornus* was recovered from a level "not much higher" than skulls 3 (*T. prorsus*, Y.P.M. 1822), 4 (= *T. serratus*, Y.P.M. 1823) and

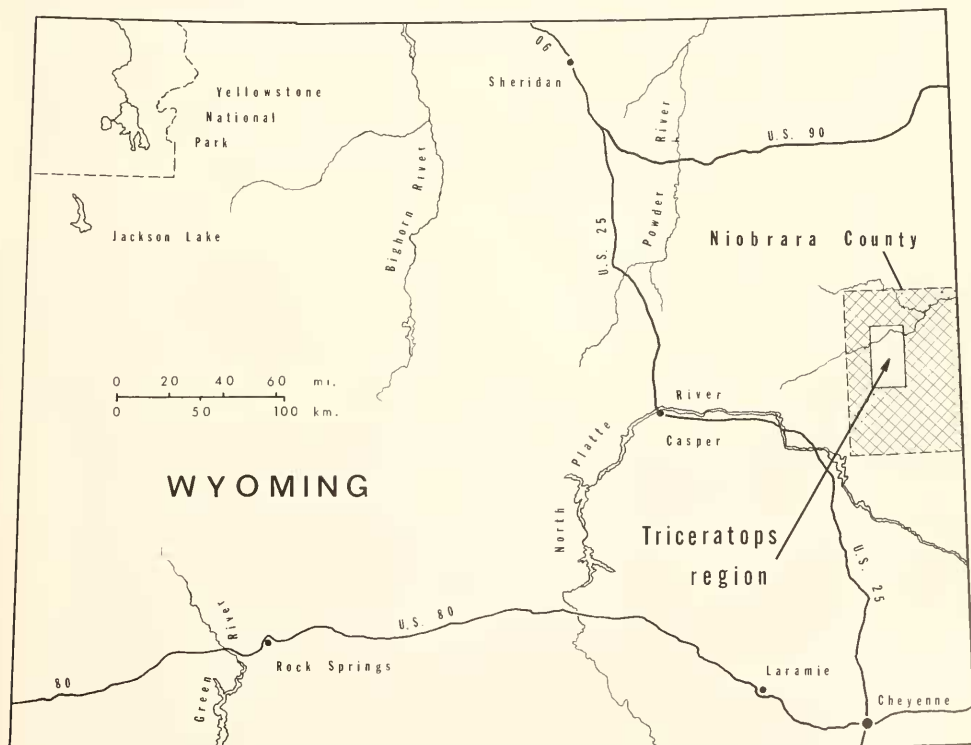
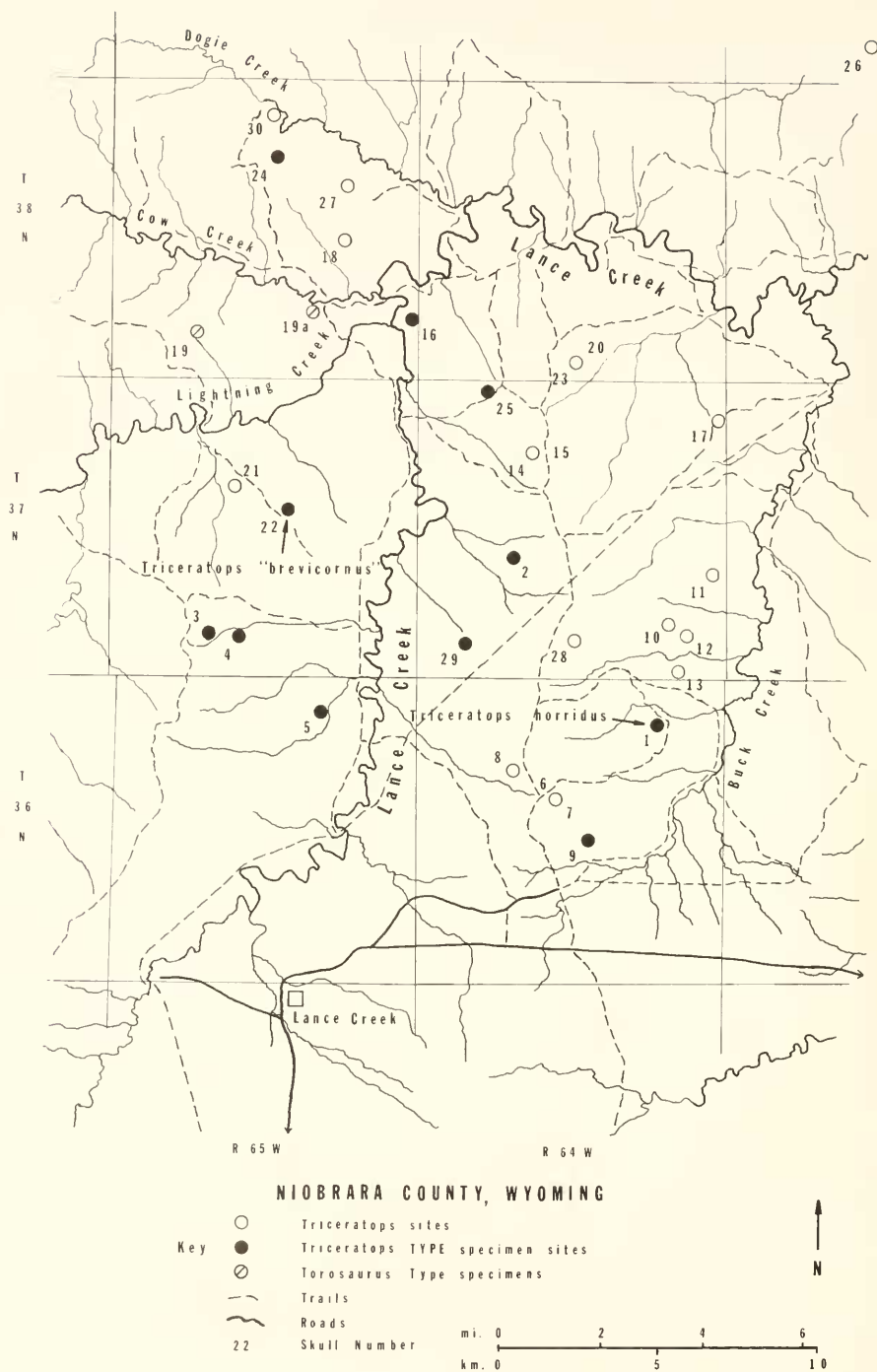


Fig. 14: Location of Niobrara County (previously part of Converse County) and the historic *Triceratops* region in relation to other landmarks within the State of Wyoming. The designated area within Niobrara County includes six Townships (see figure 15) covering approximately 216 square miles (equals 560 square kilometers).

TRICERATOPS COUNTRY U.S.A.



5 (= *T. sulcatus*, U.S.N.M. 4276). Those three specimens are the type specimens. With the exception of the type specimens of *T. horridus* (Y.P.M. 1820) and *T. obtusus* (U.S.N.M. 4720), a doubtful taxon for technical reasons, all of the Niobrara County type specimens of *Triceratops* are reported to have been recovered from levels between that of *T. prorsus* (Y.P.M. 1822) – the lowest, and that of *T. brevicornis* (originally Y.P.M. 1834) – the highest. The type specimens of *brevicornis*, *flabellatus*, *hatcheri*, *elatus*, *sulcatus*, *calicornis*, *serratus* and *prorsus* all occurred within a relatively narrow stratigraphic range. How much lower in the section the two excluded specimens (*horridus* and *obtusius*) occurred cannot be determined now. As far as we know, no exact data on this was recorded.

Considering those two low specimens, that of *T. horridus* has special interest. Although it has no formal taxonomic validity, it is significant that Lull (1933, p. 117) stated that he would refer the “type” skull of the invalid *T. ingens* (Y.P.M. 1828) to *T. horridus* “as far as can be ascertained in its present condition”, and he so listed it in his chart (1933, p. 114). The “*ingens*” skull had the highest stratigraphic position within that series, with the exception of the two type specimens of *Torosaurus* and one indeterminate specimen of *Triceratops*. If Lull’s assessment is correct, and we admit this is a moot point in view of the present state of Y.P.M. 1828, then almost the entire series of Niobrara County type specimens is sandwiched between specimens of the *T. horridus* variety.

It is unfortunate that the precise stratigraphic spacing of these specimens can no longer be established. But despite the lack of those quantitative data, it is evident that at least eight

of the 10 Niobrara “species” of *Triceratops* were collected from closely spaced stratigraphic levels. Now add to that stratigraphic distribution the very close spatial occurrence of these same specimens pointed out above. The only reasonable and logical explanation is that these specimens represent a single species.

Earlier, under the discussion of geographic occurrence, we implied that similar species of large terrestrial animals do not co-exist naturally. We summarized that reality in the preceding section on sources of anatomical variation. Please refer to Figs. 13, 14 and 15 on the zoogeography of the “type” specimens of *Triceratops*.

That brings us to the question of *T. eurycephalus*, the type and only specimen of which was collected in Goshen County, Wyoming, less than 100 miles (150 km) south of the Niobrara County *Triceratops* field. Its stratigraphic position relative to those in Niobrara County cannot be established, but the Torrington Member, from which it was collected, is considered the uppermost unit of the Lance formation.

As noted elsewhere, the distinctive breadth of the frill relative to total skull length noted by Schlaikjer (1935) in *T. eurycephalus* presented a new diagnostic parameter to be considered in the taxonomy of *Triceratops*. We note with interest the distribution of Schlaikjer’s cephalic indices relative to the ontogenetic ages of the specimens (see p. 142). Aside from this feature, which appears to range widely throughout the *Triceratops* sample regardless of age, there is no other distinctive character in this specimen. Accordingly, we are of the opinion that *T. eurycephalus* represents another individual of the single species of *Triceratops* represented by the many examples from Niobrara County.

Fig. 15: Map of the region just north of the community of Lance Creek in east central Wyoming. It is from this region that most of the type and other classic specimens of *Triceratops* were recovered by John Bell Hatcher for Yale College Museum and Professor O. C. Marsh during the years 1889 to 1892. The open and solid circles indicate the locations of the original sites of the 32 ceratopsian skulls and partial skeletons collected by Hatcher within this area. Both symbol types are labeled with the skull number, as originally designated by Hatcher, and recorded on the adjacent chart. The solid circles mark the sites of specimens that were later designated by Marsh, Hatcher or Lull as type specimens of “new” species of *Triceratops*. The specimen described here (originally *T. brevicornis*) was skull 22, and is from site 22. All the indigenous *Triceratops* types are indicated here as follows:

- | | |
|--|---|
| 1: <i>T. horridus</i> (Y.P.M. 1820) | 16: <i>T. elatus</i> (U.S.N.M. 1201) |
| 2: <i>T. flabellatus</i> (Y.P.M. 1821) | 22: <i>T. brevicornis</i> (Y.P.M. 1834 – Now B.S.P. 1964 I 458) |
| 3: <i>T. prorsus</i> (Y.P.M. 1822) | 24: <i>T. “ingens”</i> (Y.P.M. 1828) |
| 4: <i>T. serratus</i> (Y.P.M. 1823) | 25: <i>T. hatcheri</i> (U.S.N.M. 2412) |
| 5: <i>T. sulcatus</i> (U.S.N.M. 4276) | 29: <i>T. calicornis</i> (U.S.N.M. 4928) |
| 9: <i>T. obtusus</i> (U.S.N.M. 4720) | |

It is noteworthy that the sites labeled 19 and 19a produced the type specimens of *Torosaurus latus* (Y.P.M. 1830) and *Torosaurus gladius* (Y.P.M. 1831). According to Hatcher’s notes and Lull’s summary of 1915, all these specimens came from the Lance formation, the relative stratigraphic positions are recorded in Lull (1915, 1933). Map drafted from United States Geological Survey map NK 13–2, Newcastle, Wyoming, 1962 Edition. Specimen data from Lull, 1915. Abbreviations: R. = Range, T. = Township. Note: Buck Creek is now called Crazy Woman Creek and Dogie Creek was spelled Doegie Creek in the 1880’s.

SYSTEMATIC REVISION OF *TRICERATOPS*

Class Reptilia

Subclass Archosauria

Order Ornithischia Seeley 1888

Suborder Ceratopsia Marsh 1890

Family Ceratopsidae Marsh 1888

Genus *Triceratops* Marsh 1889 (*Ceratops* Marsh 1888, *Sterrhophus* Marsh 1891, ? *Diceratops* Hatcher 1907)

Diagnosis: Large ceratopsian with three facial horn cores — two large brow horns composed of postfrontals and frontals and a single nasal horn core composed of a separate ossification or as an outgrowth of the nasals; lengths and curvature of horns vary; nasal horn size variable, but always shorter than brow horns, directed up and forward and usually not curved; brow horns project up and forward, any transverse or posterior curvature variable, but usually not present; frill short compared with some other ceratopsids (postorbital length = 1.1 to 1.4 times preorbital length), composed of parietals and long squamosals extending to posterior frill margin; frill margins not horned or bearing spikes, but may support blunt epoccipital bones; frill is not fenestrated except for small lateral and superior temporal fenestrae proximally; postfrontal fontanelle usually closed; antorbital fenestra narrow and slit-like; external naris very large; large edentulous turtle-like beak composed of rostral and premaxillae above and prementary below; jugal expanded into a robust ventral

process overlapping the quadrate; mandible massive with a strong laterally placed coronoid process of the dentary; teeth “two-rooted” and compressed into large longitudinal shearing batteries; twenty-four presacral vertebrae, including eight cervicals; first four cervicals co-ossified; lumbar lacking; sacral series includes posterior dorsals and proximal caudals up to a total of 10 or 11 segments; limbs as in other ceratopsids.

Species: *horridus* Marsh 1889

Diagnosis: Same as for the genus.

Synonymy: *flabellatus* Marsh 1889, *serratus* Marsh 1890, *prorsus* Marsh 1890, *elatus* Marsh 1891, *calicornis* Marsh 1898, *brevicornis* Hatcher 1905, ? *hatcheri* Lull 1905, *eurycephalus* Schlaikjer 1935. Also, *obtusus* Marsh 1898 and *albertensis* Sternberg 1949 are probable synonyms.

Type: Y.P.M. 1820 (Pl. XXVI, Figs. 24, 25, 27; Hatcher, Marsh and Lull, 1907). Incomplete skull, lacking the posterior and lateral parts of the frill and portions of the circumorbital region, and with fragmentary lower jaws. This is Hatcher's “Skull No. 1”, discovered by E.B. Wilson and C.A. Guernsey and collected by J.B. Hatcher in 1889.

Horizon: About the middle of the upper half of the Lance formation, Late Cretaceous.

Locality: Section 2, T. 36 N., R. 64 W. Niobrara County, Wyoming, U.S.A.

CONCLUSIONS

As one of the finest skulls of *Triceratops* in existence, the specimen in the Bavarian State Collections in Munich deserves special attention. Important also, are the rarely found postcranial elements that are not often preserved with the more massive (and attractive) skull. Both are described and illustrated here.

Review of the history of discovery, the localized occurrence of most of the type specimens, the anatomical bases for

discriminating the multiple “species”, together with our understanding of the zoogeography of current large terrestrial animals leads to the conclusion that only one species is represented by the numerous *Triceratops* specimens from the Lance formation and equivalent strata. It is proposed that *Triceratops horridus* is the only valid species, the holotype being the fragmentary skull — Y.P.M. 1820.

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PLATES

Plate 1

Triceratops horridus Marsh, holotype specimen of *T. "brevicornus"* Hatcher, Lance Formation, Niobrara County, Wyoming, formerly Yale Peabody Museum (Y.P.M. 1834), now the Munich specimen (B.S.P. 1964 I 458).

- 1: Skull and mandible in left lateral view,
- 2: mandible in dorsal view,
- 3: skull and mandible in right lateral view.

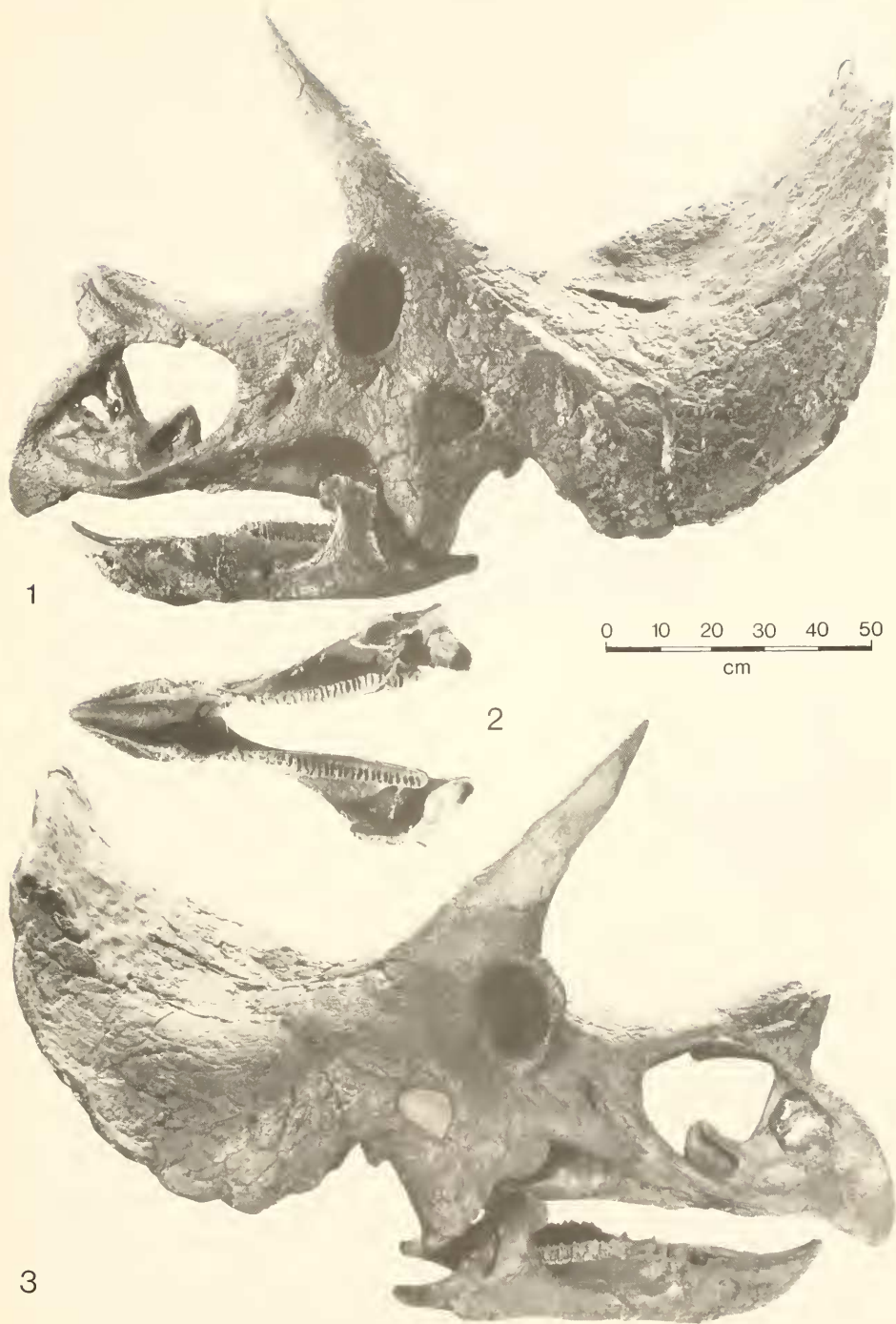


Plate 2

Triceratops horridus, holotype specimen of *T. "brevicornus"* (B.S.P. 1964 I 458), cervical vertebrae, Lance Formation, Niobrara County, Wyoming. 0,25 natural size.

1: Coossified complex of the first four cervicals (syncervicals) in posterior (1 a), right lateral (1 b), anterior (1 c) and dorsal (1 d) views.

2: Fifth cervical in anterior (2 a), left lateral (2 b), right lateral (2 c), posterior (2 d) and dorsal (2 e) views.

Abbreviations: c capitulum, dp diapophysis, li scar of interspinous ligament, nc neural canal, ns neural spine, po postzygapophysis, pp parapophysis, pr prezygapophysis.

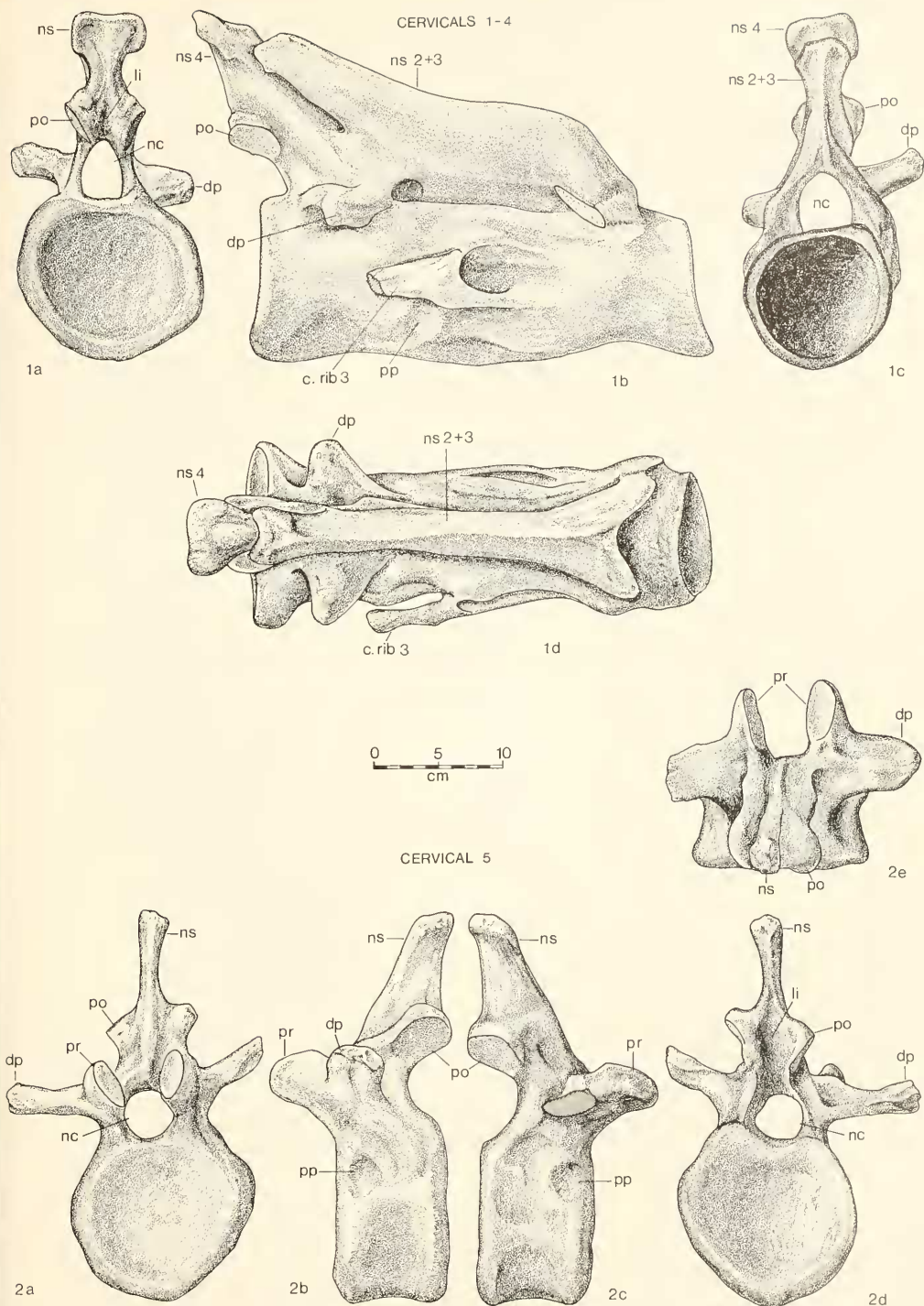


Plate 3

Triceratops horridus, holotype specimen of *T. "brevicornus"* (B.S.P. 1964 I 458), cervical vertebrae 6, 7 and 8, Lance Formation, Niobrara County, Wyoming.
From left to right in anterior, left lateral and posterior views. 0,25 natural size. Abbreviations as for plate 2.

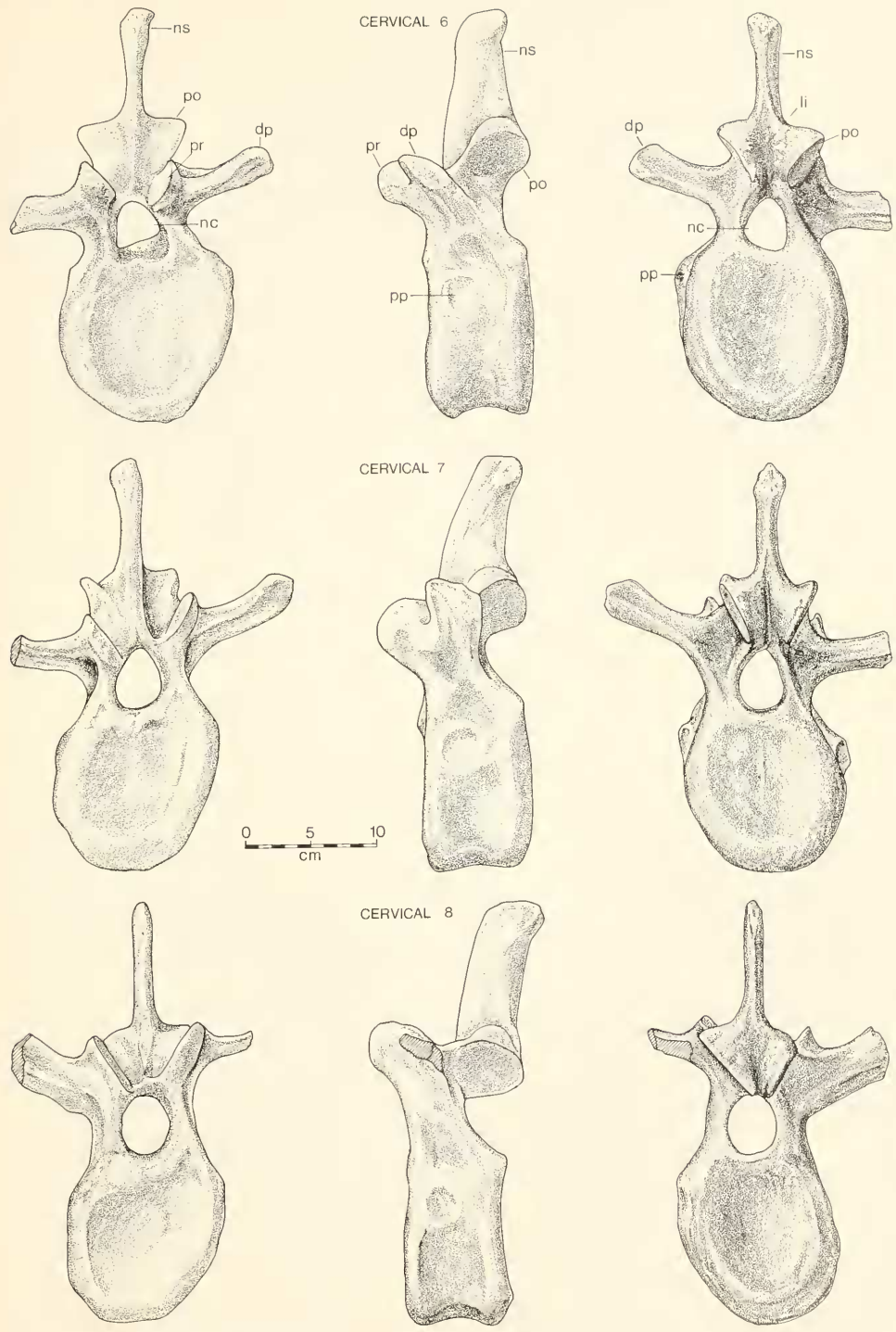
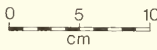
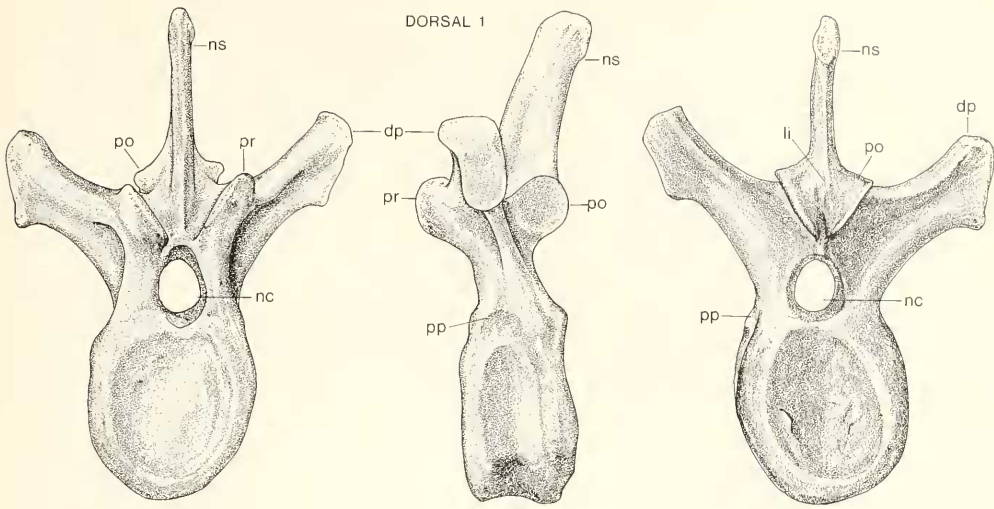


Plate 4

Triceratops horridus, holotype specimen of *T. "brevicornus"* (B.S.P. 1964 I 458), dorsal vertebrae 1 and 2, Lance Formation, Niobrara County, Wyoming.
From left to right in anterior, left lateral and posterior views. 0,25 natural size. Abbreviations as for plate 2.

DORSAL 1



DORSAL 2

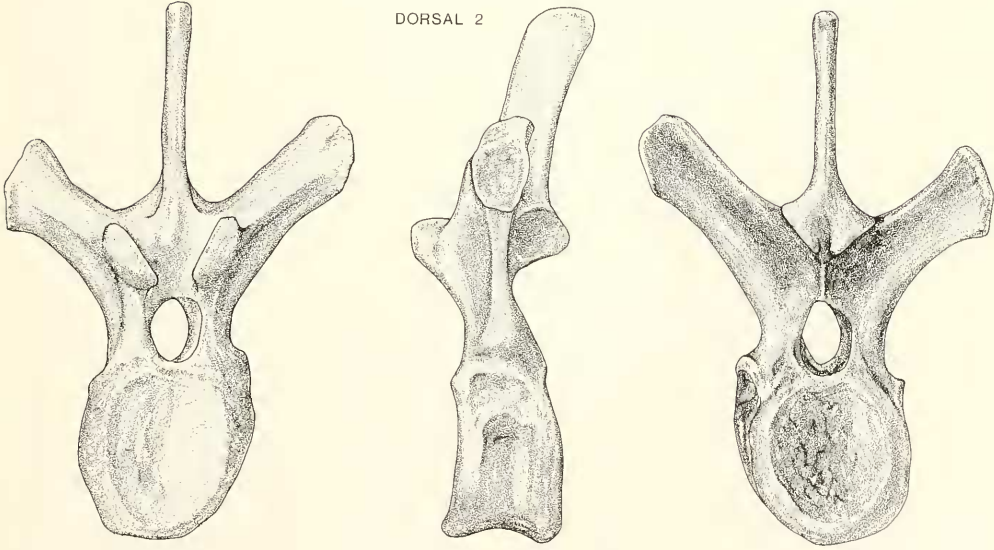


Plate 5

Triceratops horridus, holotype specimen of *T. "brevicornus"* (B.S.P. 1964 I 458), dorsal vertebrae 3 and 4, Lance Formation, Niobrara County, Wyoming.
From left to right in anterior, left lateral and posterior views. 0,25 natural size. Abbreviations as for plate 2.

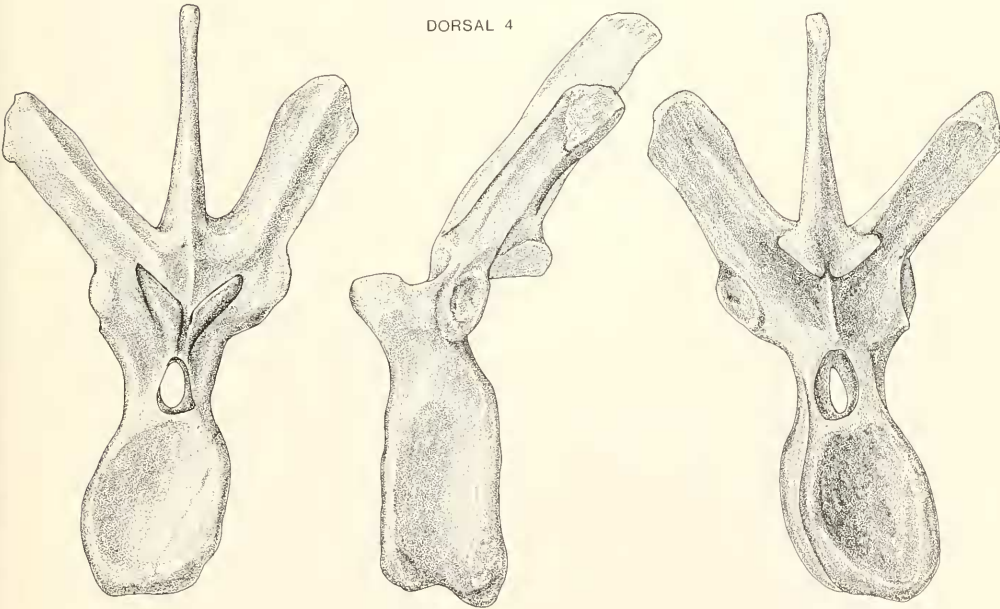
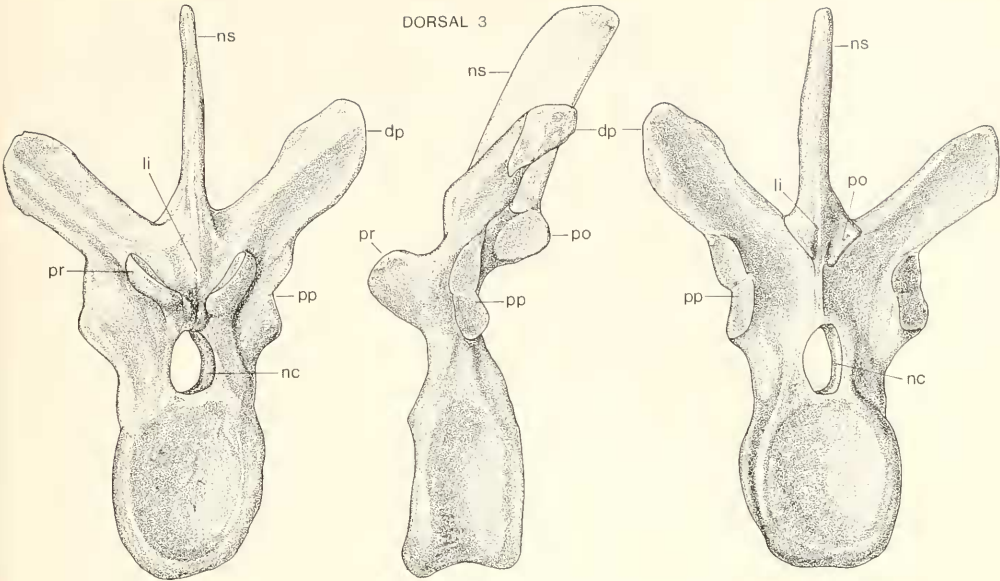
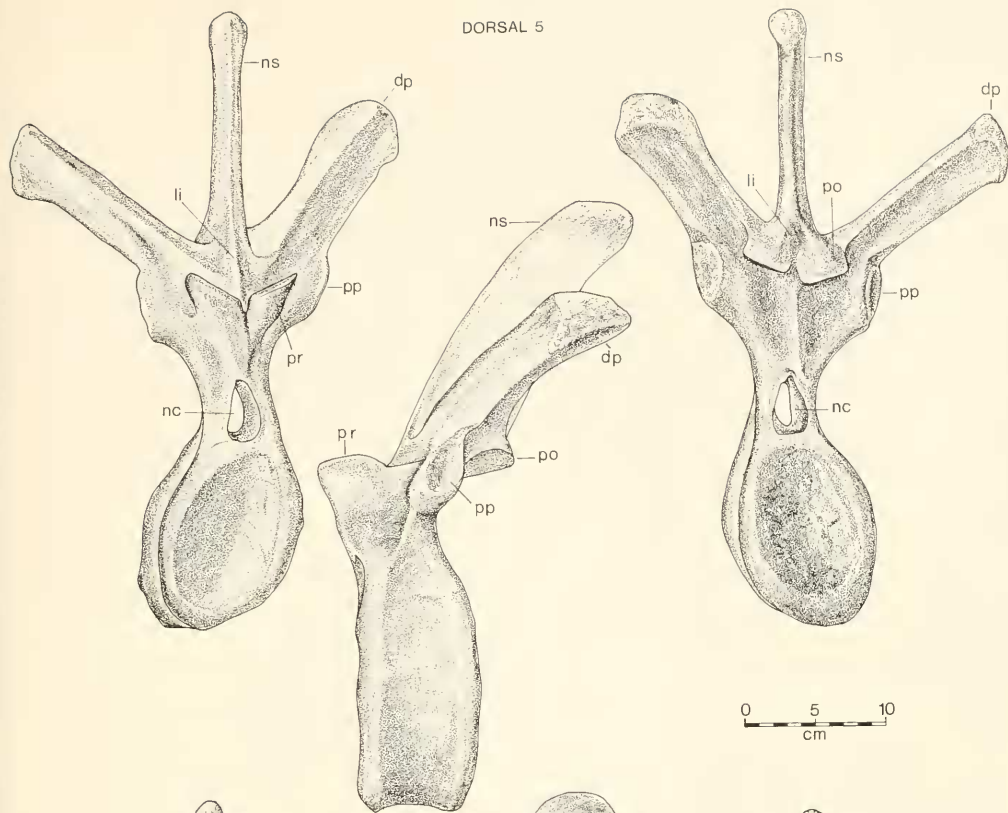


Plate 6

Triceratops horridus, holotype specimen of *T. "brevicornus"* (B.S.P. 1964 I 458), dorsal vertebrae 5 and 6, Lance Formation, Niobrara County, Wyoming.
From left to right in anterior, left lateral and posterior views. 0,25 natural size. Abbreviations as for plate 2.

DORSAL 5



0 5 10
cm

DORSAL 6

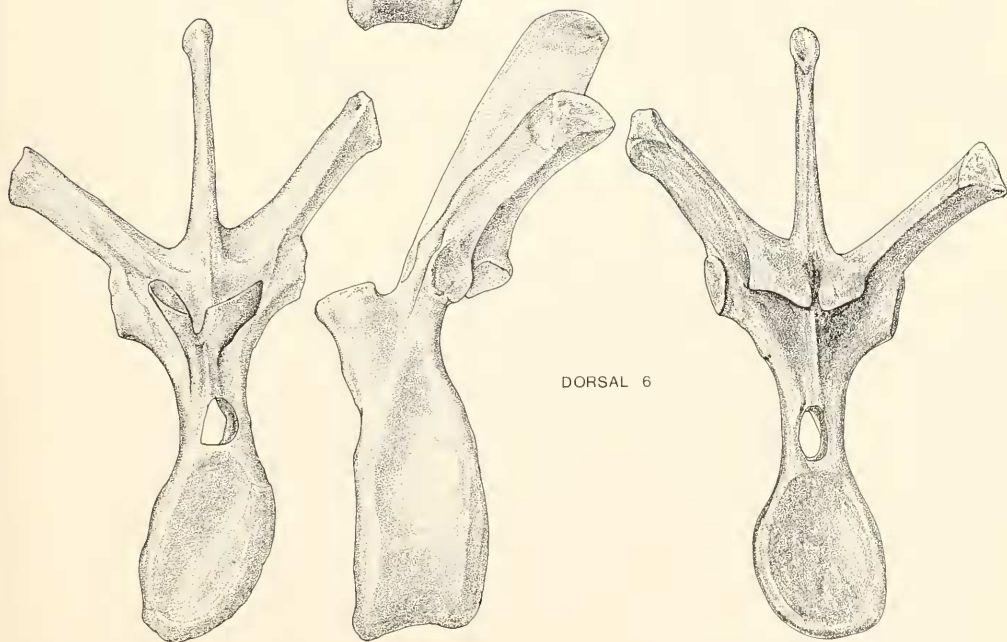
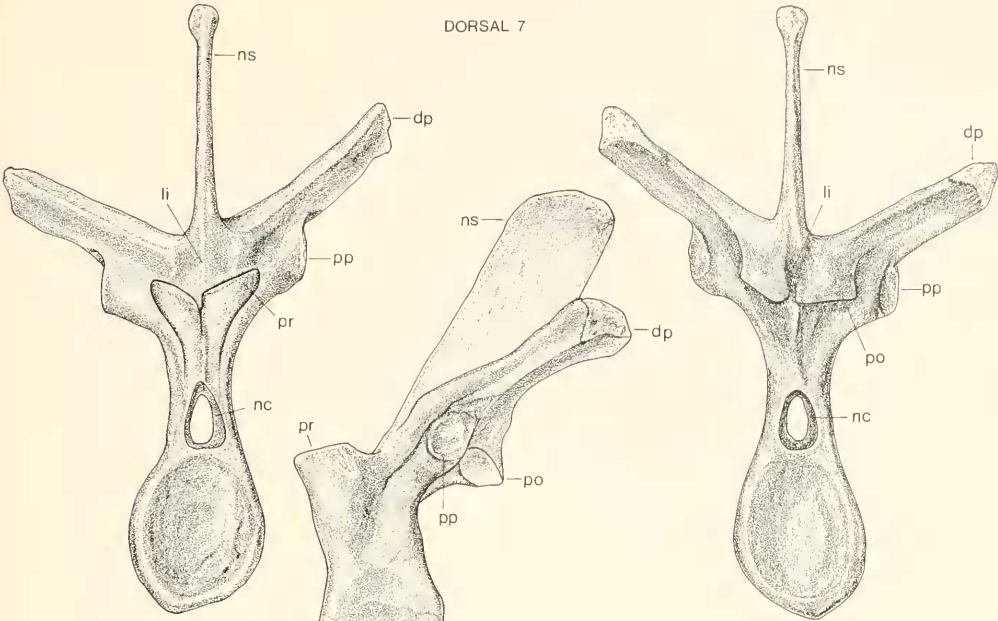


Plate 7

Triceratops horridus, holotype specimen of *T. "brevicornus"* (B.S.P. 1964 I 458), dorsal vertebrae 7 and 8, Lance Formation, Niobrara County, Wyoming.
From left to right in anterior, left lateral and posterior views. 0,25 natural size. Abbreviations as for plate 2.

DORSAL 7



0 5 10
cm

DORSAL 8

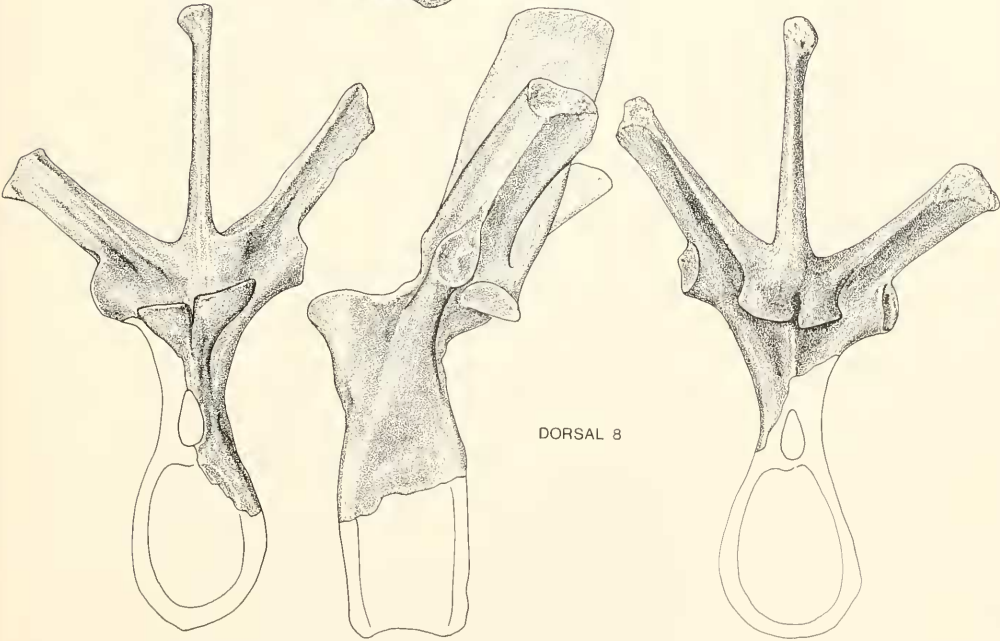


Plate 8

Triceratops horridus, holotype specimen of *T. "brevicornus"* (B.S.P. 1964 I 458), dorsal vertebrae 9 and 10, Lance Formation, Niobrara County, Wyoming.
From left to right in anterior, left lateral and posterior views. 0,25 natural size. Abbreviations as for plate 2.

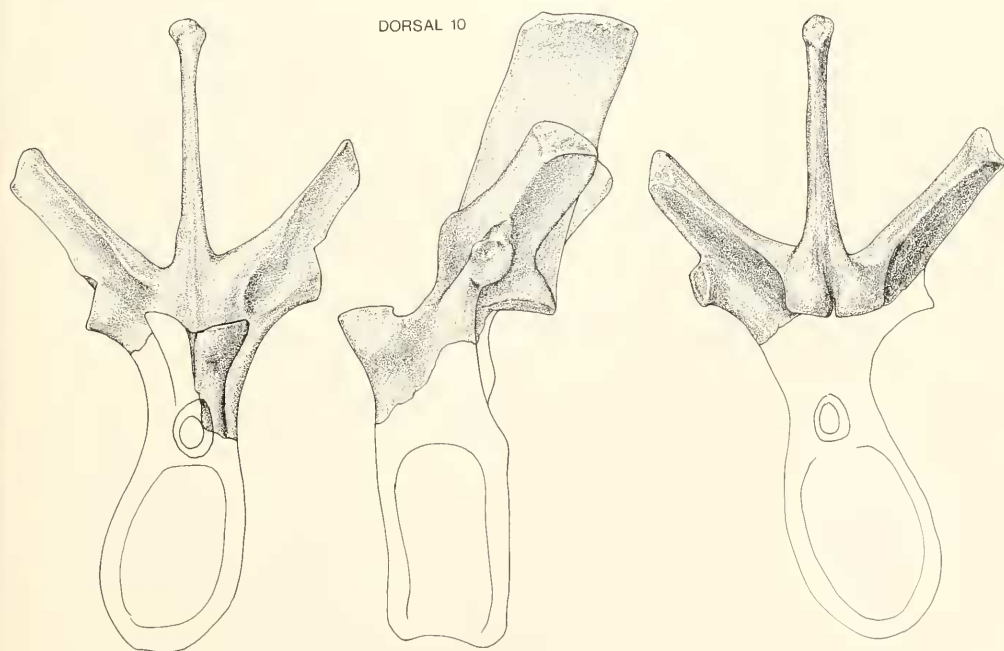
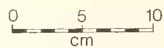
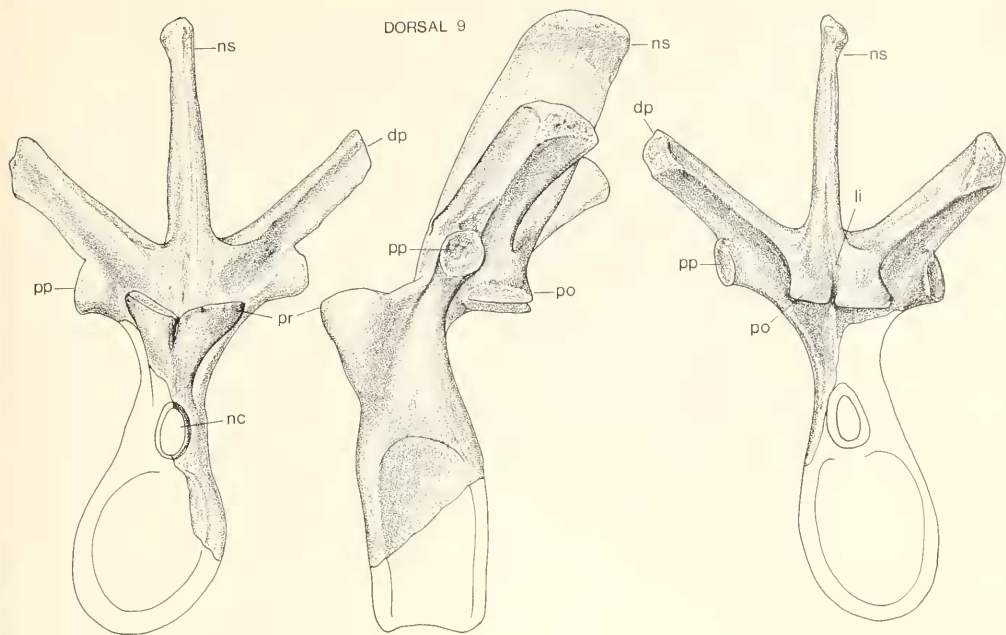
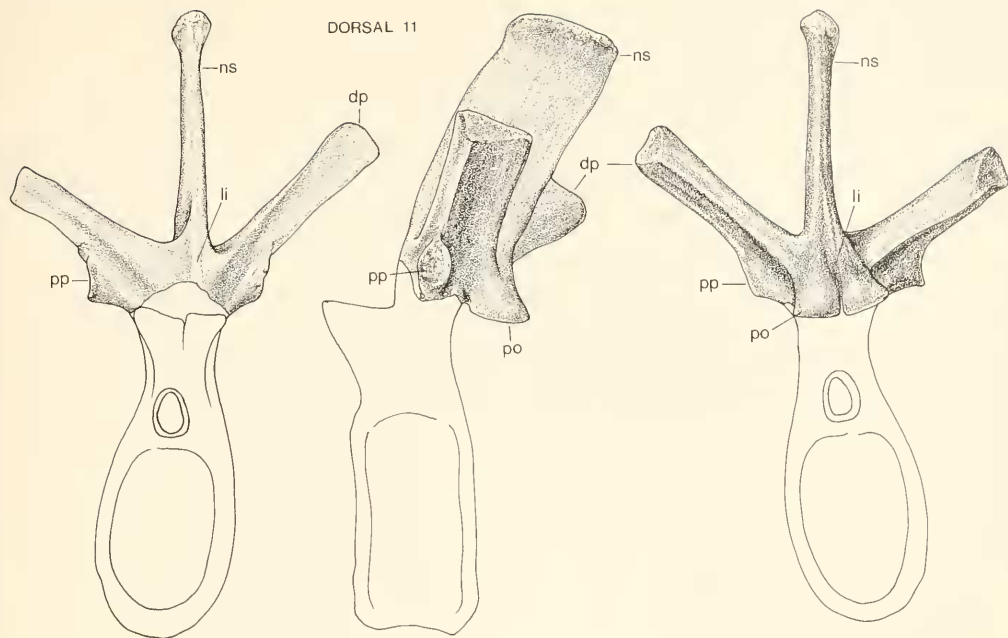


Plate 9

Triceratops horridus, holotype specimen of *T. "brevicornus"* (B.S.P. 1964 I 458), dorsal vertebrae 11 and 12, Lance Formation, Niobrara County, Wyoming.

From left to right in anterior, left lateral and posterior views. 0,25 natural size. Abbreviations as for plate 2.

DORSAL 11



0 5 10
cm

DORSAL 12

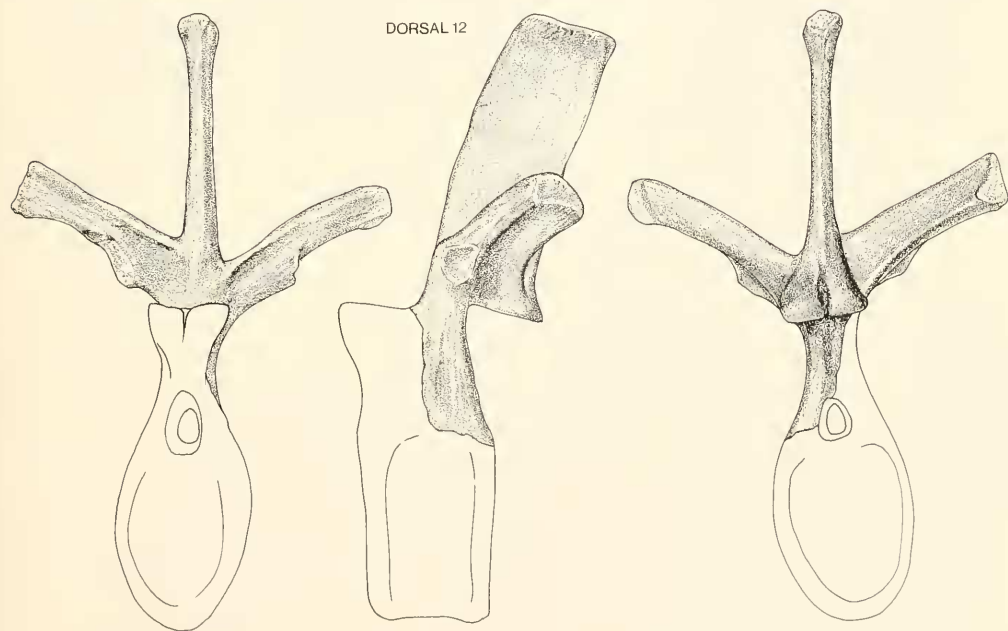


Plate 10

Triceratops horridus, holotype specimen of *T. "brevicornus"* (B.S.P. 1964 I 458), dorsal vertebrae 13 and 14, and mid caudal vertebra, Lance Formation, Niobrara County, Wyoming.
From left to right in anterior, left lateral and posterior views. 0,25 natural size. Abbreviations as for plate 2.

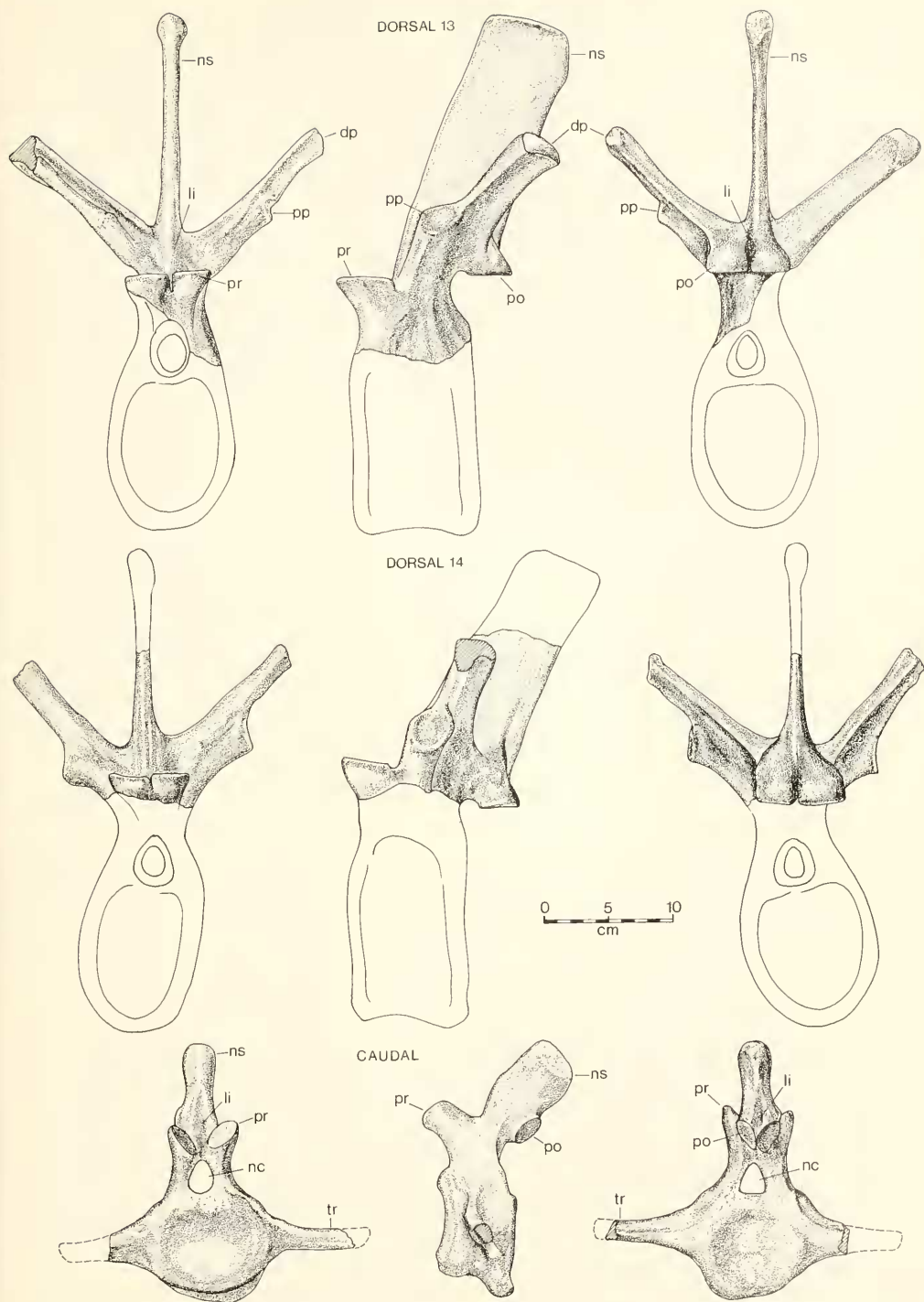


Plate 11

Triceratops horridus, holotype specimen of *T. "brevicornus"* (B.S.P. 1964 I 458), Lance Formation, Niobrara County, Wyoming.

1: Right pubis in lateral (1 a), dorsal (1 b) and medial (1 c) views, as preserved. Abbreviations: aba anterior border of acetabulum, ppp postpubic process.

2: Cervical rib 4, left, lateral view.

3: Cervical rib 5, left, lateral view.

4: Cervical rib 6, left, lateral view.

5: Cervical rib 7, left, lateral view.

6: Cervical rib 8, left, lateral view.

Abbreviations: ca capitulum, tu tuberculum. 0,25 natural size.

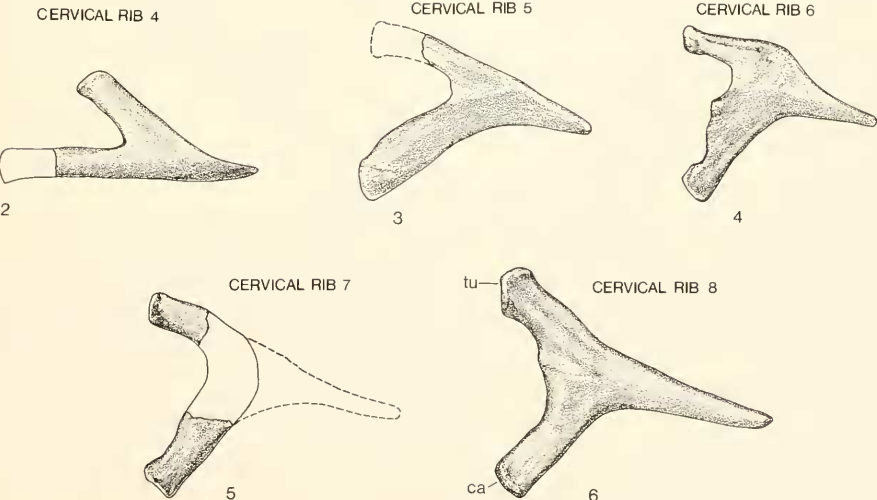
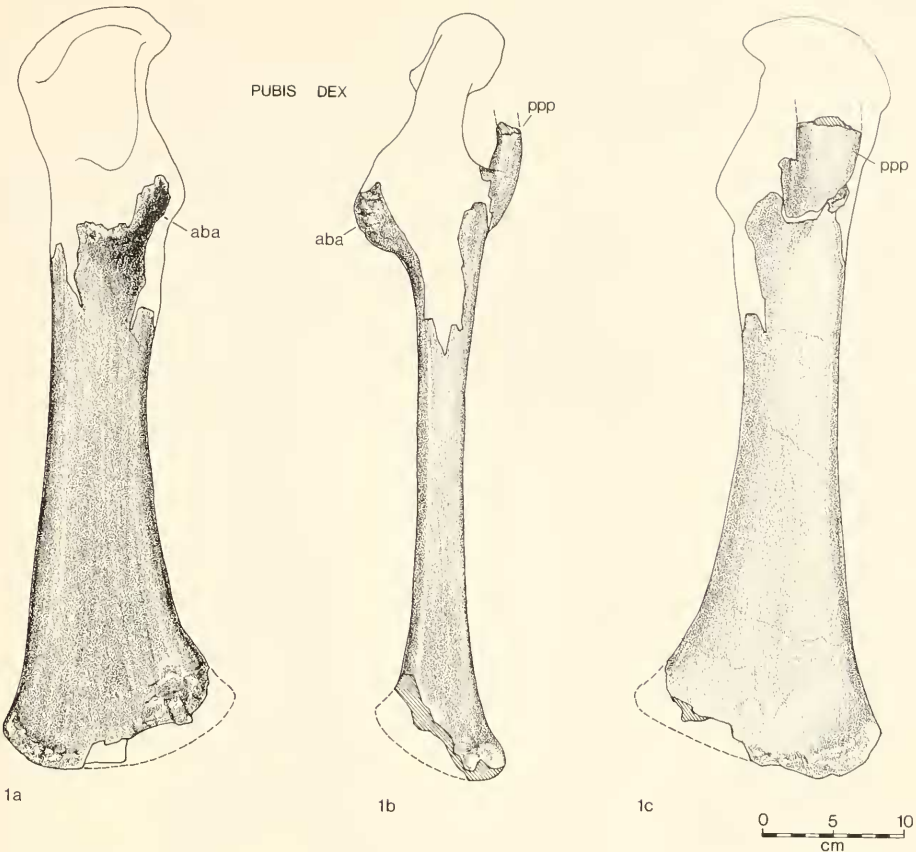


Plate 12

Triceratops horridus, holotype specimen of *T. "brevicornus"* (B.S.P. 1964 I 458), dorsal ribs 2, 3, 4, 5 and 6 as preserved, Lance Formation, Niobrara County, Wyoming, 0,25 natural size. Abbreviations as for plate 11.

